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ILLINOIS BIOLOGICAL MONOGRAPHS

VOLUME XII

PUBLISHED BY THE UNIVERSITY OF ILLINOIS

g URBANA, ILLINOIS

EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ
FRED WILBUR TANNER
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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XII

April, 1929

No. 2

EDITORIAL COMMITTEE

STEPHEN ALFRED FORBES

FRED WILBUR TANNER

HENRY BALDWIN WARD

PUBLISHED BY THE UNIVERSITY OF ILLINOIS
UNDER THE AUSPICES OF THE GRADUATE SCHOOL

DISTRIBUTED

JUNE 18, 1930

MORPHOLOGY, TAXONOMY, AND
BIOLOGY OF LARVAL
SCARABAEOIDEA

WITH FIFTEEN PLATES

BY

WILLIAM PATRICK HAYES

Associate Professor of Entomology in the University of Illinois

Contribution No. 137 from the Entomological Laboratories of the
University of Illinois

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INTRODUCTION

The larvae of the superfamily Scarabaeoidea are commonly called white grubs or grubworms. Forbes, writing in 1891 on insects of this group in relation to their life histories, said that "it is necessary that the observer should learn to distinguish species of these insects in the grub and larval stage." Among the numerous genera, the species of which are usually more readily recognized in the adult form, there are many species that are almost indistinguishable from one another in the larval stage. To identify them it is usually necessary to rear the specimens. This requires a long period of time and often involves dangers of loss from one cause or another during the period of rearing. In a number of groups, especially in the subfamily Melolonthinae, the life-cycle covers a period of from two to three years, and in northern latitudes even four years. Such a long larval stage makes rearing difficult. Moreover, since the larval life is spent under the surface of the soil, it is difficult to maintain rearing conditions as near normal as necessary. Not only do the representatives of the various subfamilies differ in length of life in various localities, but they may exhibit wide degrees of variance even in the same localities.

Rapid strides have been made in our knowledge of the life histories of these insects within the last twelve years (1917-29), and it is becoming increasingly more important, as we survey the great differences exhibited, that we be able to recognize the larval forms. As with all other groups of insects, our knowledge of the developmental stages lags behind our knowledge of the adults. This is especially true in the fields of morphology and taxonomy and to a lesser extent in the field of biology. Prior to the studies by Davis and others, which have materially increased our knowledge of the group, most of our knowledge of the biology of these insects has been based on fragmentary accounts scattered in the literature. The present work deals with morphological, taxonomic, and biological studies of the various species of white grubs. The morphological studies have aided materially in constructing the diagnostic keys to the various genera which are included. Life-history studies made by the writer, some of which have, in part, appeared in different publications, are here brought together and briefly summarized to make the present work as nearly a complete unit as possible.

ECONOMIC IMPORTANCE

Of the four families, Passalidae, Lucanidae, Scarabaeidae, and Trogidae, comprising the superfamily Scarabaeoidea (or Lamellicornia), the family Scarabaeidae is the best known and most important. The others have only slight economic importance.

The family Passalidae, which inhabits decaying wood, is represented in tropical forests by numerous species but in North America by only one species, *Passalus cornutus* Fab. Some species of this family are of biological interest because of a certain degree of social organization ascribed to them, the adults being known to attend the larvae and care for them throughout their period of development to maturity. The adults chew the woody food and prepare it before feeding it to the larvae. The hastening of decay in rotten logs can be said to be a beneficial phase exhibited by this group of insects.

The Lucanidae, or stag-beetles, exhibit wide sexual differences in the adult stage. Their larvae, like the Passalidae, live in rotten logs or roots. About 300 species of Lucanidae occur throughout the world, but only 30 species are recorded by Leng (1920) from North America. Aside from their biological interest, the unique stridulation structures of the larvae and the benefits incurred from the hastening of decay, the family can be considered of little importance.

The family Trogidae is one of our newer families, having recently been raised to its present position from subfamily rank in the Scarabaeidae. Of the genera occurring in North America, the genus *Trox* is the most important. The larvae of *Trox* are scavengers and are usually found in dried, decomposing, animal matter or on the soil under such matter. Little is known of their life history.

The Scarabaeidae in the adult stages are known as chafers, May beetles, June bugs, dung beetles, and dor beetles. They constitute a large family with about 14,000 species known from all parts of the world. The family is divided into two categories, or groups, the Laparosticti and the Pleurosticti. The Laparosticti are, for the most part, coprophagous in habits. The Coprinae, Aphodinae, and Geotrupinae are the better known subfamilies with coprophagous habits. A few of the Coprinae are known to be myrmecophilous and live as symphiles in the nests of ants. The coprophagous habit is, by far, the most important. The group Pleurosticti contains a large number of important economic insects. These occur in four subfamilies: the Melolonthinae, the Rutelinae, the Dynastinae, and the Cetoniinae.

The larvae of the subfamilies here considered are recognized in many parts of the world as pests of planted crops and are almost universally known as "white grubs." One of the most notorious members of the group is the European "Hanneton," *Melolontha melolontha*, which has been

known for over a century as a destructive enemy of the roots of crops. It belongs to the subfamily Melolonthinae, to which our common American species of May beetles, or June bugs, are assigned. Certain species of Phyllophaga (Lachnosterna), both adults and larvae, are perhaps the most destructive members of the family in North America, and their injury is too well known to require extended discussion.

In some of the states west of the Mississippi the greatest loss from white grubs occurs where the larvae of *P. lanceolata* (Say) attack the roots of wheat and often destroy thousands of acres in a single season. Considering the country as a whole, most of the principal crops as well as native prairie pastures, meadows, and lawns have suffered injury from various species. In some localities gardens suffer. Potatoes especially have paid a heavy toll in the last few years. Strawberry beds have been the object of regular attacks, and ornamentals of all kinds, particularly those recently set out, have been seriously damaged. Many lawns have been killed by the grubs, and serious loss has occurred in the bluegrass pastures. According to Davis (1918), alfalfa is usually considered free from injury, but it has been found damaged in a number of localities. In attacking this crop, the grub enters the tap-root an inch or two below the surface of the soil, excavates a cavity, and burrows upward and downward in much the same manner as some of the root-boring insects.

Among the Rutelinae, two species, *Pelidnota punctata* L. and *Cotalpa lanigera* (L.) are notably injurious in the United States. The damage caused by the spotted grapeleaf beetle, *Pelidnota punctata*, to the foliage of grapes during some years attracts considerable attention, but the larvae, living in rotten wood, such as logs and old stumps, can be regarded as beneficial because their activities in these situations hasten decay. The goldsmith beetle, *Cotalpa lanigera*, has been reported by Davis (1916) as ranking next in importance to the species of Phyllophaga. He says that the grubs in Michigan are destructive to raspberry bushes, strawberries, corn, and grass. Other native species of Rutelinae treated here are not of so much economic importance, but *Anomala innuba* at times becomes numerous. The beetles of this species do some damage to the kernels of growing wheat, which they attack while "in the milk," and the grubs feed on the roots of various plants. Two important imported members of this subfamily are the Japanese beetle, *Popillia japonica* Newm., and the Asiatic beetle, *Anomala orientalis* (Waterhouse).

Among the representatives of the Dynastinae dealt with herein, *Ligyroides relictus* Say is not known to be a crop pest, but a near relative, *Ligyroides gibbosus* DeGeer, is an important enemy of carrots and domesticated sunflower crops, and is known as the carrot beetle.

The best known American species of the Cetoniinae are the bumble flower beetle, *Euphoria inda* L., and the green June beetle, also called the

fig eater, *Cotinis* (*Allorhina*) *nitida* L. The bumble flower beetle is a somewhat general feeder, being found upon flowers, eating the pollen, and upon corn stalks where it feeds on the green cob by sucking the juices. It also occurs on peaches, grapes, and apples, and occasionally its injury becomes serious. The larva is not known to cause damage. The green June beetle, on the other hand, is a pest in the grub stage, feeding upon the roots of grasses and often doing immense damage to tobacco plantings, lawns, and golf courses (Chittenden and Fink, 1922). Two species of *Euphoria*, *E. sepulchralis* Fab. and *E. fulgida* Fab., are neither of great importance economically. They feed in the adult stage on the pollen and nectar of flowers. The beetles of *E. sepulchralis* feed on the tips of ears of corn, making way for further injury by the green June beetle, *Cotinis nitida*. The species of *Osmoderma* pass their developmental periods in decaying wood, as do also the larvae of *Trichiotinus* (*Trichius*), and are only of minor significance.

HISTORICAL REVIEW

Some members of the families Scarabaeidae and Lucanidae have been known from ancient times. The Romans frequently hung the mandibles of Lucanus on the necks of children or wore them in the form of armulets to ward off disease. In Germany, Lucanus was known as the "fire-starter" because it was said to carry live coals into houses with its pinchers, thereby starting conflagrations. The people would often cooperate in their efforts to drive them away. The sacred beetle of Egypt has made the family Scarabaeidae renowned, and many interesting tales and superstitions have been connected with it. These myths and legends are too numerous to be discussed here and, except for historical value, are irrelevant in a work of this nature.

The meaning and origin of the word Scarabaeus is clouded in doubt and uncertainty. Papis, a grammarian of the eleventh century, says the word comes from *cabus* or *caballus*, meaning horse, because the insects according to the ideas of the times were thought to be born from the cadaver of a horse. Bochart derives the word from *chaphas*, which signifies an excavator, in view of the characteristic action of coprophagous species. Fabricius derives it from the Greek *to dig*, and MacLeay from the Greek *to scratch* or *scrape*. Mulsant, Martini, and others accept Aristotle's interpretation, which derives it from a Greek word signifying an insect that is unknown to us.

The first splitting of the group, as defined by Linnaeus, occurred when Scopoli (1763) separated the genus Lucanus from Scarabaeus. Fabricius, Olivier, and others followed with many new genera, until ultimately the two groups represented by Scarabaeus and Lucanus were elevated to family rank under the superordinal appellation Lamellicornia, a term which was first used either by Lamarck (1817) or Latreille (1817). According to

Burmeister, it is not known which of the two was the originator of the term, but it is generally attributed to Latreille, to whom is also credited the origin of our modern conception of the family group. The termination *-idae* was for the first time generalized in entomology by MacLeay in 1819. Leng (1920) in his recent check list of North American Coleoptera considers the Lamellicornia under the superorder Scarabaeoidea, recognizing three families, Scarabaeidae, Lucanidae, and Passalidae. The recent supplement to Leng's list, by Leng and Mutchler (1927), considers the subfamily Troginae as of family rank, so that as now constituted there are four recognized North American families, namely, Scarabaeidae, Lucanidae, Passalidae, and Trogidae.

There have been several European attempts to work out the classification of larval stages of the Scarabaeoidea. The anatomical descriptions of individual species are fairly numerous in scattered foreign works, but the problem in America has been given little attention. Until recently there has been no attempt at a general classification, and isolated descriptions are scarce and in many instances inadequate.

TAXONOMIC LITERATURE

A study of the distinguishing characters of American lamellicorn larvae has been a long-felt need. Moreover, their economic importance makes such a study of extreme value. It is highly desirable to be able to recognize the different genera at least, and, when possible, the species belonging to the genera. Forbes (1894) in his Eighteenth Report (p. 97) stated that "life-histories are not sufficiently different to make discrimination of species a matter of practical importance, and for economic purposes, consequently, the white grubs may usually be classed as one." A little later in the same report (footnote, p. 105), in speaking of the verification of life-histories, he says "it is necessary that the observer should learn to distinguish species or at least groups of species of these insects in the grub and larval stage." Forbes then pointed out differences between *Ochrosidia* (*Cyclocephala*) and *Phyllophaga* (*Lachnosterna*) grubs. The latter genus was divided into three groups: the *hirticula-rugosa*, *fusca-inversa*, and *gibbosa* (now *futilis*) group. Except for the work of Forbes and scattered isolated descriptions, no attempt was made in this country to characterize the various groups of the family until Böving (1921) published a short key dealing with several allied genera of the green Japanese beetle (*Popillia japonica*), which is based in part on the work of Schiödt (1874). This generic key indicated the distinguishing characters of one European and five American genera.

In contrast to the work done in America on this group, a number of European papers are available which, although dealing with but few genera occurring in this country, are of value in a study of this nature.

Chapuis and Candeze (1855, p. 452) noted that the habits and metamorphosis of no group of European beetle larvae were as well known as the lamellicorns. The first to attempt a classification of these larvae was DeHaan (1836), who used both external and internal characters to distinguish eight genera. DeHaan made use of the malpighian tubules, and in his work the drawings of the alimentary canal are especially good. The next attempt at classification was made by Mulsant (1842), who compiled a key based on external characters alone. The same year (1842) Burmeister published in a large measure the groupings of DeHaan. Erichson (1848) presented a study of the group and used an arrangement of the families, which we now recognize as subfamilies. Erichson's key is also found in the catalogue of coleopterous larvae in which Chapuis and Candeze in 1855 brought together the references to descriptions of larvae known at that time. Schiödte's classical work on the larvae of Coleoptera appeared in 1874 in several parts, of which Part VIII deals with the lamellicorn larvae. The drawings in this work are indeed excellent. Three years later Perris (1877) published his well-known work which contains the most complete key to genera that we have. He added many new descriptions of lamellicorn larvae. Recently Ritterschaus (1927) has described somewhat completely the morphological details of *Anomala aenea* Geer and *Phyllopertha horticola* L. This work is perhaps the first to give any detailed consideration to the epipharynx of white grubs. More will be said concerning this work later. A recent paper by the writer (1928) on the epipharynx of the larvae contains a preliminary generic key, including a few species, based in great part on characters of the epipharynx. This key with corrections, additions, and emendations is used in the present work as a basis of generic distinction.

BIOLOGICAL AND ECOLOGICAL LITERATURE

In America the life-cycles of the Lucanidae and Passalidae are little known and not thoroughly worked out. The Trogidae are as yet untouched. The economic species of the Scarabaeidae have, in recent years, become better known, although scarcely anything has been done on the coprophagous forms. Previous to 1916, our knowledge of the life-cycles of the American species of Phyllophaga was confined to the work of Chittenden (1899) who reared a single specimen of *P. fervida* (*arcuata*) and to those of Davis (1913) who reported a two-year life-cycle for *P. tristis*. In 1916, Davis discussed the length of life of 18 species of the genus, but did not determine the length of the various stages. This work is of great importance to our knowledge of the group. Smyth (1917) published the results of life-history studies of certain Porto Rican species of Phyllophaga, in which our first account is available concerning the length of the various instars.

The writer has from time to time published life-history studies of various species of the family. The life-cycle of *P. lanceolata* was noted as having a

two-year period of development with quite varied habits from the majority of species of Phyllophaga. In another paper (1920) seven species, *futilis*, *rubiginosa*, *vehemens*, *crassissima*, *rugosa*, *implicata*, and *submucida* of the same genus were reported as having a two-year or a three-year life-cycle. This was followed by a more comprehensive report (1925) of the studies made on ten other species of Phyllophaga and some other members of the family belonging to different subfamilies. Along with these were recorded data on the development of three species of Rutelinae, one Dynastinae, and two Cetoniinae. In the present work these studies will be brought together for the purpose of comparison.

In the subfamily Rutelinae the species of the tribe Anomalini require one year for completion of their life-cycle. *Anomala binotata* and *A. innuba* were found by the writer (1918 and 1925) to have a one-year period. The same time is required for *Strigoderma arboricola* (Hayes, 1921). The Oriental *Anomala* and the Japanese beetle are likewise known to have a one-year life-cycle. In the tribe Rutelini, of the subfamily Rutelinae, the life-history is longer. It has been shown (Hayes, 1925) that *Pelidnota punctata* requires two years to mature and *Cotalpa lanigera* needs either two or three years.

All the species of the Dynastinae so far studied by the writer and by others require but a single year to develop, with the exception of *Strategus quadrifovius* (Smyth, 1916) which requires more than one year but considerably less than two years. The species of the subfamily Cetoniinae, as far as known, usually occupy one year in the completion of growth. *Cotinus nitida* requires one year (Chittenden and Fink, 1922) while the writer (1925) recorded the same length of life for *Euphoria fulgida* and *E. sepulchralis*.

MATERIALS AND METHODS

The methods of study for the data herein reported are of two distinct types, biological and morphological. The biological end of the problem demanded rearing methods which enabled the handling of the immature stages over a long period of time; while the morphological studies, made primarily for taxonomic results, required the collection and preservation of definitely known larvae and some slight laboratory technique.

On account of their subterranean habits and long period of development, white grubs are difficult to rear to the adult stage. The difficulty arises not only from their prolonged life-cycle, but also because of the many parasitic fungi and other diseases attacking the grubs while being reared under artificial conditions. In order to be sure of having some specimens mature, it was necessary to handle large numbers of eggs and larvae; and in order to study molting, it was necessary to keep them isolated. Davis (1915) and Smyth (1917) have devised methods of rearing white grubs and May beetles, and suggestions of these two writers were fol-

lowed in this work. These methods with some others are here briefly summarized.

To procure eggs it was only necessary to confine the beetles over a few inches of damp, well-packed soil. Any sort of cage could be used, but most of them were one-gallon tins, half-filled with moist earth, the tops being perforated. The leaves of various trees were frequently supplied for food by merely placing them on the surface of the soil. The earth was sifted or carefully gone over for eggs every second day. It was found that disturbing the soil every day produced a tendency for the beetles to lay fewer eggs. The eggs were transferred to individual cavities in closely packed, dampened soil in one-ounce or two-ounce tin salve boxes, where they were kept until hatched. From 25 to 50 eggs can be cared for in each box in this manner. Upon hatching, each grub was placed in a one-ounce salve box where it was kept until it matured or died. These salve boxes, at times numbering over 5,000, were kept in the rearing cave described by McColloch (1917) in which there was a nearly constant temperature, and thus the grubs were not subjected to the daily fluctuations of temperature in the outdoor insectary. The grubs were examined, with the aid of student assistants, twice a week during the warmer parts of the year, once a week in spring and autumn, and once a month during the winter months, and at each examination the soil was changed and new food (generally a few grains of wheat, which soon germinated) was added, except in the winter when the food was omitted. When a grub reached the prepupal stage, the soil in the box was tightly packed and the grub placed in a depression to simulate a pupal cell. These prepupae were then isolated from the others and examined daily to obtain the dates of pupation and maturity.

All of the species whose life histories are herein discussed were thus handled with the exception of *Pelidnota punctata*, whose habit of living in rotten logs during the larval stage made some changes in the above procedure necessary. This species, the most difficult of any to rear, failed to thrive in individual salve boxes in which rotting pieces of wood were substituted for the grains of wheat. Only one specimen was thus reared. Other specimens, however, were reared in decaying wood placed in one-gallon tins and left undisturbed. This method does not permit the making of observations to determine the molting periods.

One other slight deviation from the general method of rearing was necessary in the case of *Ligyroides relictus* and the *Euphoria* grubs whose larval stage is passed in manure and other decaying vegetable matter. In these cages, instead of feeding wheat grains to the grubs, which, however, they will eat, the soil in which they were placed was made more to their liking by adding to it an equal amount of dried manure.

The material for morphological and taxonomic work was obtained in great part during the course of life-history studies carried on by the writer.

The majority of the specimens were reared from eggs laid by definitely determined beetles. However, certain species which can be distinguished by their habits or the habitat in which they live were studied when their identity was certain. As an example, large grubs found in rotting haystacks can be determined with comparative surety as *Ligyroides relictus* (Say), and other instances could be cited. The molted exuviae of reared grubs were preserved and have proved quite helpful in this study. They possess the advantage of having all the chitinous parts of the mouthparts intact without the presence of muscles and tissues, and this dispenses with necessity of putting them through a clearing process. The molted exuviae are transparent and readily studied and dissected under the microscope.

ACKNOWLEDGMENTS

The collections of the Illinois State Natural History Survey have been used freely through the courtesy of Dr. T. H. Frison, and quite recently the collections of Prof. J. J. Davis, now the property of the U. S. National Museum, have been received for study through the courtesy of Professor Davis, Dr. Adam G. Boying, and Mr. S. A. Rohwer. The latter collections consist mainly of a large number of reared species of Phyllophaga but include also some other genera, three or four of which were not in the writer's collections. Most of the drawings were made by one of my students, Mr. Carl Mohr, through the aid of a grant from the Graduate School of the University of Illinois.

Besides acknowledging indebtedness to the aforementioned persons who have rendered aid in this work, the writer desires to express his gratitude to the officials of the Kansas Agricultural Experiment Station, especially to Professors J. W. McColloch and George A. Dean, under whose direction the life-history studies were carried out.

MORPHOLOGY

The following descriptions of larvae were made in most instances from reared specimens concerning whose identification there is no doubt. A few species were studied which are readily recognizable by their habitus, habitats, or habits, and were not reared because there is reasonable certainty of their correct identification.

The external anatomy of American species of white grubs has been given but slight consideration. Few complete or detailed descriptions of the morphological features are available. With the exception of a few widely scattered descriptions of some known larvae, little has been done. The writer recently (1927) presented somewhat detailed morphological descriptions and figures of the immature stages of *Anomala kansana* H. and McC. Böving's work (1921) on the Japanese beetle has already been mentioned, but nowhere have any comprehensive comparisons been made of American species. Grandi (1925) has presented comparisons of three Italian species. Reference has been previously made to European works on scarabaeid larvae.

The larvae of the Scarabaeoidea (Fig. 1 to 12) are quite similar to one another but easily distinguished from other beetle larvae. The body is elongated, subcylindrical, and in most cases normally bent in the form of a letter C. From this shape is derived the term "scarabaeiform" used to describe this type of larva. The body in many species is nearly constant in diameter from the anterior to the caudal end. In the Cetoniinae (Fig. 11) the caudal end is frequently enlarged, while in many Rutelinae (Fig. 8) it is tapering. The body is distinctly differentiated into a well-formed head and a series of twelve segments making up the thorax and abdomen. The three segments of the thorax bear three pairs of well-formed legs, except in *Passalus* (Fig. 3) which has but two well-developed pairs. The legs are not as important organs in locomotion as they are in digging. In some Cetoniinae the legs are not used at all for walking. Such species crawl upon their back by the aid of body contractions, in which they are assisted by the erect setae with which the body segments are provided. When placed upon their feet, these larvae invariably turn over on their backs in order to move themselves along. The head is more heavily chitinized than the rest of the body, which is paler in color, and the integument is somewhat transparent. The body segments are usually divided into a series of deep folds forming subsegments or annulets. There are usually three subsegments in most of the segments, although in a few species they are indistinct or lacking. The segments in the Lucanidae are less conspicuously subdivided, and in *Passalus* there are no annulets present.

The general body form of some of the coprophagous beetles is distinctly "hump-backed" in outline. This is seen in such genera as *Canthon*, *Copris*, *Pinotus* (Fig. 1), and *Onthophagus* (Fig. 4). Such species usually develop in balls or packs of manure formed by the parents at the time of oviposition.

THE HEAD AND ITS APPENDAGES

The head (Fig. 13 to 24) is hypognathous, that is, situated at right angles to the long axis of the body and with the mouthparts directed ventrad. It is more strongly chitinized than the remainder of the body and varies considerably in color with the various species, ranging from light-yellow or tan in some through all degrees of brown almost to black. The Rutelinae and Melolonthinae contain some of the lighter forms; while the Dynastinae, as represented by *Xyloryctes*, have darker heads. The general form is convex or subglobose (Fig. 13 *et al*) and usually symmetrical, although some species (Fig. 23) are decidedly asymmetrical.

The head capsules of *Phyllophaga crassissima* (Fig. 16), *Ligyris gibbosus* (Fig. 19), *Cotalpa lanigera* (Fig. 20), *Euphoria inda* (Fig. 21), and *Canthon laevis* (Fig. 13) are typical representatives of five separate subfamilies of the Scarabaeidae. In general, they bear a striking resemblance to each other. In color, they vary from a light to a dark tan almost brownish. The size of the head is variable, depending of course upon the instar of the grub and also the species concerned. It has been suggested that the relative size of the head capsule, being thought constant in the various instars, would be of value in distinguishing the different species; but careful observation shows a gradual increase in size between molts.

The cephalic aspect of all species presents the same general gross features, in which is evident the epicranial suture (Fig. 13 *es*) dividing the epicranium, or vertex, and bounding with its branching arms (*ea*) the lateral margins of the front, or frons (*f*). Between the arms of the epicranial suture, on the frons, in *Canthon laevis* (Fig. 13), *Euphoria inda* (Fig. 21), and others, is an extended Y-shaped depression resembling a second epicranial suture and setting off an area quite similar to the adfrontal area found in some lepidopterous larvae. This impression may be a secondary suture. If this condition is an extension of the true suture, it is so closely fused that in *E. inda* there is scarcely any trace of it on the inner surface, while in *C. laevis* the inner surface presents a decided ridge, or carina, which does not extend into the arms. The epicranial suture splits at the time of molting and usually the split is continued into the arms of the Y. In *C. laevis*, however, the split does not extend into the arms, reaching only to the point of branching. In *C. laevis* and in *E. inda* there is a tendency for splitting in the secondary Y. An examination of *E. inda* alone would lead to the conclusion that the secondary Y is merely a depression in the front; but if *C. laevis* is the more primitive of the two, the presence of

the carina may indicate that a suture is disappearing during specialization.

Coincidentally, these two species present a series of four rounded depressions, two on the front and two on the vertex near the arms of the epicranial sutures. At first these suggest remnants of ocelli. In the genera *Trichiotinus* and *Strategus* in which ocelli do occur, they are located near the base of the antennae and seem to have no relation to the depressions in *Canthon* and *Euphoria*. The two depressions on the front are perhaps the external evidence of the points of attachment of the dorsal arms of the tentorium.

The clypeus (Fig. 13 *clp*) adjoining the front is trapezoidal in shape and to it is attached the flap-like labrum (*lab*) with its laterally rounded sides. Laterad of the clypeus and labrum are the prominent mandibles (*md*). The antennae (*ant*) are the only segmented appendages evident on the cephalic aspect, except in *Canthon laevis* where the maxillae may protrude from under the mandibles and thus expose the maxillary palpi. In no case are the labial palpi discernible from this view.

In a caudal view (Fig. 92, 93) with the head removed from the thorax the relatively large occipital foramen (*of*) is seen to be bounded by the fused areas of the postgenae and occiput. Surrounding the foramen is a slight ridge, represented in the drawings by the dotted lines, to which is attached the cervical membrane. The labium is divided into three regions. The submentum (*sm*) is the basal, or proximal, sclerite to which is joined distally the mentum (*m*), and in turn the stipula (*st*) joins the mentum. The maxillae (*mx*) lie laterad of the mentum, and under the maxillae lie the mandibles (*md*).

The heads of the species of the other three families of the super-family—Lucanidae (Fig. 23), Passalidae (Fig. 24), and Trogidae (Fig. 22)—present no striking differences from those of the Scarabaeidae just described. There is a greater tendency for the head to be asymmetrical which is quite pronounced in the head of *Sinodendron* (Fig. 23) and less so in *Trox* (Fig. 22). The head of *Passalus* (Fig. 24) is more like the Scarabaeidae in being nearly symmetrical but is somewhat broader in proportion to its height.

In all species, the head is the most heavily chitinized area of the body. The surface is frequently smooth and impunctate, in other species it is rugose or rugulose. A few setae may be noted. There are frequently four rather conspicuous setae on the clypeus.

ANTENNAE

Three pairs of segmented head appendages are evident from the caudal aspect, the antennae, maxillary palpi and labial palpi. The number of antennal segments has been a matter of discussion. The proximal seg-

ment in nearly all species is fused to the head and not articulate. Some writers disregard it as a segment while others count it as a true division of the appendage. Osten-Sacken (1874) in speaking of the antenna of *Pleocomma* says it is "three-segmented" and does not consider the basal, or fused, region which he termed the "scapus." Schiödt (1874) also disregards it and considers it a "palpiger." Later workers have called it a separate segment, and in this study it will be considered as the first antennal or basal segment. The view of Perris (1877, pp. 93-94) on the number of antennal segments is presented below:

D'après Erichson et les savants naturalistes de Lyon, ces organes seraient composés de trois à cinq articles, le premier n'étant pour eux qu'une saillie tuberculeuse qui simule un article. Je ne puis me ranger à cette opinion. Je ne prétends pas dire qu'elle constitue une appréciation erronée de la structure des antennes, mais comme cette saillie tuberculeuse existe dans toutes les larves, que si, par suite de sa retractilité ou autrement, elle laisse quelquefois place au doute, elle présente habituellement la physionomie d'un véritable article; comme aussi la plupart des auteurs, y compris les entomologistes éminents que je viens de citer, lui ont le plus souvent donné ce caractère dans leurs descriptions, je crois qu'il faut le lui maintenir sous peine d'avoir à rectifier presque tout ce qui a été dit jusqu'ici sur les antennes. Je ferai remarquer en outre que, si cet article basilaire devait être retranché, il serait inexact de dire que les antennes des larves de Lamellicornes ont de trois à cinq articles, car alors il y aurait des larves qui, avec l'article basilaire, en auraient six, ce que je n'ai jamais vu.

In most subfamilies of the Scarabaeidae, the antennae are five-segmented (Fig. 95, 96). The first, or basal, segment being short and conical, the second, third, and fourth are much longer than the first and vary somewhat in size with the different species. The fourth segment at its distal end is frequently extended into a more or less acute or obtuse process (Fig. 95). The fifth segment is usually shorter than the penultimate. In some species it is of fair size and tapers to a point or else ends bluntly. In many of the coprophagous species the last segment is greatly reduced in size and appears almost like a small papilla (Fig. 13) on the end of the fourth segment. Frequently, large sensory pits are evident in the fifth segment. These vary in number in different species in which they occur.

Among some of the coprophagous species of Scarabaeidae, in the Trogidae, and in some Lucanidae, there are but four antennal segments, and in most instances of this sort the terminal segment is small and papilla-like. The antennae of *Passalus cornutus* (Fig. 94) in the Passalidae are but three-segmented. The proximal segment is short but greatly widened, being several times wider than long, or about equal in width to the length of the third segment. The second segment is less widened, somewhat longer, and somewhat conical in shape. The third or distal segment is two or three times longer than wide and somewhat pointed. The composite form of all three segments presents the appearance of a rather uniform cone.

CLYPEUS AND LABRUM

The clypeus presents little that is striking in variation in the different species. It is usually somewhat trapezoidal or subrectangular in outline, and frequently its lateral margins are slightly emarginate, while the proximal and distal margins are usually subparallel. It is much wider than long, and in many species the distal half is less heavily chitinized, with a somewhat sharp line of demarkation, presenting the appearance of a clypeal suture, thus dividing the structure into a preclypeus (Fig. 18, *pc*) and a postclypeus (Fig. 18, *psc*).

In *Canthon laevis* Drury (Fig. 13) the clypeus (*clp*) is about twice as wide as it is long, the anterior and posterior margins are subparallel, and the lateral margins are emarginate and converge slightly distally. The labrum (*lab*) is rounded on the sides, and the anterior margin is distinctive, certain subfamilies having a double emargination that causes the median lobe to appear quite prominent. In none of the forms observed is the labrum exactly symmetrical.

A study of *Canthon ebenus* Say indicates its similarity to *C. laevis*. The clypeus and labrum are quite similar, having as their most conspicuous feature the biemarginate labrum. *Onthophagus pennsylvanicus* Harold has the same general features of the clypeus and labrum with the biemarginate anterior margin and prominent median lobe. Perris (1877, pl. 3) figured *Copris lunaris* L. with a labrum of this type, while Osten-Sacken (1862) figured *Pinotus* (*Copris*) *carolina* (L.) with an excision in the prominent median lobe. In a study of *P. carolina* specimens before the writer, this excision of the median lobe is not present (Fig. 90, 127). The margin is biemarginate with a conspicuous median lobe showing no excision as in Osten-Sacken's drawing.

The labrum in the species of *Aphodius* studied—probably *A. fimetarius* (L.)—is biemarginate, asymmetrical, and trilobed (Fig. 14). It is nearly as long as wide. Schiödt (1874) has figured the labrum of *Aphodius rufipes* (L.) which is quite similar. Both resemble the form of the labrum in *Canthon*.

Phyllophaga crassissima (Blanch.) (Fig. 16) has the clypeus of somewhat the same general shape as *Canthon laevis*. It is trapezoidal in form with the lateral sides less deeply emarginate. The labrum lacks the lobes on the anterior margin and is somewhat pointed. It is as long as broad and circular in outline. The anterior margin is slightly crenate. *Phyllophaga lanceolata* (Say) has much the same general form of clypeus and labrum with no apparent external difference.

An undetermined species of *Diplotaxis* has the clypeus and labrum about twice as broad as the length of either single part. In order words, the combined length of clypeus and labrum is equal to their breadth. The clypeus is trapezoidal in shape, and the labrum is broadly oval. Schiödt

(1874) figures the clypeus and labrum of *Rhizotrogus fallenii* Gyll. and *Serica brunnea* L. with a somewhat different form, especially in the shape of the clypeus. The same is true of his figure of *Melolontha vulgaris* Fab.

The clypeus of *Cotalpa lanigera* (Fig. 20) is nearly three times as broad as long. The anterior and posterior margins are parallel, while the lateral margins are deeply emarginate and converge posteriorly. The labrum is almost as long as broad, subcircular in outline, but not as pointed anteriorly as in *Phyllophaga*. Both sclerites are larger than in most species. There is a striking resemblance in these sclerites to *Polymoechus brevipes* Lec. except for a proportionately smaller size and the absence of the deep emarginations on the lateral margins of the clypeus.

Anomala binotata Gyll. and *A. kansana* (Fig. 18) have a clypeus without lateral emarginations. It is twice as broad as long. The labrum is slightly broader than long, and the sides converge to a somewhat pointed margin. This point is not as sharp as in *Phyllophaga*. Schiödté figured *Anomala aenea* De Geer (*Euchlora frischii* Fab.) which also has the clypeus without the lateral emarginations and the labrum of the same shape as in *A. binotata* but with a more deeply rugose surface.

The clypeus and labrum of *Ligyryus gibbosus* De Geer (Fig. 19) is proportionately larger than in *Phyllophaga*, but smaller than *Cotalpa lanigera*, the increase in size over *Phyllophaga* being expressed in width. The clypeus is trapezoidal, and the labrum is broader and more of an oval than in either *C. lanigera* or *P. crassissima*.

In *Ligyrodes relictus* Say both the clypeus and labrum are much broader than long and proportionately larger. The labrum is the most broadly ovate of any of the forms observed. The broad condition of the labrum holds for *Ochrosidia immaculata* (Oliv.) and the anterior margin is noticeably crenate. In comparison with the species of *Ligyryus* the labrum is much longer proportionately. There are no important differences in the clypeus.

The clypeus of *Euphoria inda* (Fig. 21) does not converge anteriorly as in the other subfamilies, the whole being nearly a parallelogram with rounded corners. It is twice as broad as long. The labrum has about the same proportions, being broadly ovate with two anterior emarginations producing a small median lobe as in the *Coprinae* but not so prominent. *Euphoria sepulchralis* has the clypeus of the same rectangular shape and has double anterior margins on the labrum, but is somewhat smaller than *E. inda*. The same characteristics of clypeus and labrum are also found in *Stephanucha pilipennis* K., a rare species of *Scarabaeidae* that occurs only in Kansas. All of the *Cetoniinae* noted are more nearly symmetrical than other species studied.

The clypeus of *Trox* sp. (Fig. 22) is unique in being limited proximally by a conspicuously arched fronto-clypeal suture. It is divided into a precly-

peus and postclypeus as in the Scarabaeidae, but with the preclypeus somewhat less heavily chitinized. The labrum is very similar in form to that of the Coprinae.

In the Lucanidae as represented by *Sinodendron rugosum* Mann. the general form of both the clypeus and labrum approaches that of the Cetoniinae in being more nearly symmetrical. No noticeable emargination is present, but the whole is decidedly crenate, and the median lobe is lacking. The clypeus of *Passalus cornutus* Fab. (Fig. 24) is nearly twice as wide as long, and subrectangular. The labrum is subovate with a prominent median lobe on the anterior margin, in this respect resembling that of the Trogidae and the Coprinae.

EPIPHARYNX

The epipharynx, although an internal structure, is one that is easily accessible and can be examined without injury to the specimen by merely inserting a needle under the labrum and raising it up. It can also be studied in living larvae without any apparent harm being done to the individual. The characters of the epipharynx have not been given detailed consideration by previous workers. Schiödt (1874) figured the epipharynx of *Geotrupes*, and his drawing of this genus is copied here (Fig. 58). Böving (1921) has figured and briefly described the epipharynx of *Popillia japonica* Newm. Neither of these writers has attempted to name the various parts. A German worker (Ritterschaus, 1927) has described in some detail the epipharynx of *Anomala aenea* De Geer and *Phyllopertha horticola* L. She is the first to assign names to some of the various parts. Her terms will be mentioned later. The writer (1928) attempted to show the value of the epipharynx as an aid in the discrimination of the various genera. Further study has emphasized the importance of these characters, which are described below in detail because of their use in the generic keys in this work.

The epipharynx (Fig. 25 to 69) is defined as the ental wall of the labrum. Its proximal extent is limited by the tormae, which are situated at the lateral extremes of the clypeo-labral suture. However, a few of the setae and an important sensory area, located between the mesal ends of the tormae, are proximad of this suture and are thus on the ental surface of the clypeus.

The tormae (*t*) are heavily chitinized structures on the ends of the clypeo-labral suture (*clst*) which extend toward the mesal line and in some larvae of this group meet and fuse on the mesal line. In many insects they serve as a landmark in determining the extent of the clypeus and labrum when the clypeo-labral suture is indistinct or absent. In the present group of larvae, the tormae exhibit various sizes and shapes, and further study may find them of more taxonomic importance. They were useful in the separation of *Canthon* and *Onthophagus*. The lateral lobes (*ll*) and median lobes (*ml*), as here considered, apply to the lateral and distal margins

of the labrum of conspicuously biëmarginate species. The lateral striae (*ls*), occurring in Melolonthinae and a few other forms, are short transverse carinae at the bases of setae on the lateral margin. In *Phyllophaga* a second group of carinae, more distal and somewhat removed from the margin, are called submarginal striae (*sms*). On the median line and somewhat removed from the distal margin is an important area, here called the distal sensory area (*dsa*), containing various sensillia and strong chitinous spines. The structures in this region which are, in most cases, obviously strong spines were called by Ritterschaus (1927) "chitinous pegs," and the area upon which they are situated, and upon which are also found numerous pore-like sensillia, was called a "chitinous plate." The chitinous pegs are here called spines (*sp*) and the chitinous plate is the distal sensory area. The sensillia (*sa*) are located at the bases of the spines, being between them and the distal margin.

The proximal sensory area (*psa*) is the region between the ends of the tormae and in many species proximad of the clypeo-labral suture (*clst*). This region contains a strong, rounded tubercle called by Ritterschaus the sense-cone (*sc*). High magnification shows it to contain about four sensillia (Fig. 69). One of these sense-cones is described in detail in the description of the epipharynx of *Phyllophaga futilis*. On the right side of the sense-cone (left in drawings) is a variously shaped, chitinous plate (*cp*), which is not present in some species. On the left side of the sense-cone is a non-setose area which in some forms (*Phyllophaga*) contains 20 to 25 pore-like sensillia. In other species two or three sensillia are found in this area, and in still others none occur. These may be called the clypeal sensillia (*cls*) since they are usually on the clypeus. The remaining surface of the epipharynx is covered with variously arranged articulate setae (*st*), which are usually so arranged as to leave a clear, non-setose area in the center of the epipharynx. Frequently there are interspersed among these setae numerous groups of more delicate, non-articulate spines, especially in the region of the clypeo-labral suture.

Coprinae

Tribe Scarabaeini.—The epipharynx of *Canthon laevis* Drury (Fig. 55) is symmetrical and rather strongly developed and is rather densely covered with strong, hooked setae. The lobe is continued on the ental surface into a prominent, rounded process which bears six shorter setae. There is a central pair of setae arranged transversely, and laterad of these on each side is another pair arranged longitudinally. Still farther laterad are two pit-like structures which somewhat resemble alveoli from which setae have been removed but which are more probably sensoria. The lateral lobes are rather densely covered with long, slender, curved setae. Mesad of these on the ental aspect is located a group of not over a dozen more robust, but shorter, setae which are recumbent, their apices being directed mesad. These are apparently unequal in number on the two sides, with a few more present on

the right than on the left side. Behind, or proximad, of the median lobe in cleared specimens, is a dark, transverse, oval structure which probably would not be apparent in fresh specimens. Near the clypeo-labral suture a few slender setae are grouped on each side; they are recumbent and their points are direct mesoproximad. The tormae are not as well developed as in some other scarabaeid larvae. They appear strongly curved on the sides, and each extends on its mesal end transversely across the epipharynx to meet and fuse with the torma of the other side.

Tribe Coprini.—*Copris tullius* Oliv. (*anaglypticus* Say) also has the labrum symmetrical, strongly trilobed, and biemarginate (Fig. 64). The following description is made from a single specimen whose details are difficult to make out. Its median lobe bears four long setae hooked at the tips and also some shorter setae. The lateral lobes have only a few short setae. No distinct distal sensory area can be distinguished, and there is apparently a group of short setae arranged in the form of a circle. Near the clypeo-labral suture a darker area may be the sense-cone of the proximal sensory area. Other than the circle of setae only a few short, scattered setae are apparent on the ental surface of the lateral lobes. The tormae appear branched, one of the branches being long and extending far onto the clypeus. The epipharynx of *Onthophagus* (Fig. 67) shows quite a different arrangement of the tormae and a somewhat similar circular group of setae in the central area. The distal margin is provided with intermixed long and short, strongly hooked setae.

Aphodinae

Tribe Aphodini.—The species of *Aphodius* (Fig. 56) considered here was taken in large numbers from manure. None having been reared, the specific identity is uncertain, but from the large size of the grubs it is probably *Aphodius fimetarius* (L.), which is one of our largest and most common species. The epipharynx bears comparatively few setae both on the margin and on its inner surface. The margins are smooth proximally but rather irregular distally where they are produced into a broad, single lobe. The widest area is about in the middle, where a single articulate seta is situated with another slightly disto-mesad. Between the broadest point of the lateral margins and the distal lobe six setae, two long and four short, are found on each side. The distal lobe bears two long and four short setae on the margin and about four short setae remote from the margin. Behind the median lobe on each side are two irregularly triangular chitinized areas. Between these and immediately distad of a prominent circle of short chitinous processes, or spines, are two sense-cones. The circle of chitinous processes, or spines, at first glance resembles setae, but they are blunt at their tips, non-articulated, and at the base of some of the distal spines there is an indication of a sensory pore. This circle extends to the clypeo-labral suture.

The tormae meet and fuse on the middle line, whence a chitinous process extends distad to the center of the circle of spines and then expands slightly on the end. On the clypeus are two small chitinous plates found near the fused tormae.

Geotrupinae

Tribe Geotrupini.—No specimens of this genus were available. The drawing of *Geotrupes stercorarius* L. (Fig. 58) is a copy of Schiödte's drawing. In general it is somewhat similar in shape to *Canthon laevis*, being symmetrical and trilobed. The inner aspect has comparatively few setae. The median lobe is strongly produced on the inner aspect. Its margin shows eight strong setae, and eight others, apparently recumbent and directed proximad, are found just within the margin on the inner aspect. A strongly curved, transverse, darker area is proximad of these spines, and two series of small setae, semi-circular in arrangement, are proximad of this darker area. The median lobe is produced into a blunt, rounded process which crosses the clypeo-labral suture. The surface of the lateral lobes bears setae that are shorter and stouter than those of the lateral margins. They are, as in *Canthon*, unequal on the two sides, with a few more present on the right side than on the left. They are recumbent and their apices are directed mostly toward the meson. The tormae are not shown in Schiödte's drawing.

Glaphyrinae

The epipharynx of *Amphicoma* sp. (Fig. 61) is described from specimens in the Davis collection from Hadley, Mass., collected May 29, 1916, by H. E. Smith. Unlike most of the *Laparosticti*, the labrum is only slightly trilobed and only faintly biemarginate. On the margins, both distal and lateral, there are interspersed long and short setae, the long ones being several times longer than the short ones. The median lobe bears the distal area, which is almost on the margin and which contains about twelve sensillia in the form of small, rounded pores. The pores seem to be set off from the rest of the epipharynx by a darker, chitinous, semi-circular band which bears a few setae. The remaining surface of the epipharynx is covered with rather densely placed setae arranged in a circle, with the larger and stronger setae on the distal rim of the circle. In the cleared circle and proximad of the larger setae are a few small rounded areas that may be sensillia or trichopores. The right torma is extremely long, reaching far beyond the median line. The left torma is much shorter. The proximal sensory area, which is behind the right torma in the area formed by a strong curve of the torma, is composed of a strong tubercle-like sense-cone, with two smaller cones to the right. A few minute spines of varying sizes are to be seen proximad of the right torma, and two or three pore-like sensillia are mesad of the sense-cone.

Melolonthinae

Tribe Sericini.—The epipharynx (Fig. 31) is described from specimens in the Illinois Natural History Survey collection, determined as *Serica* sp. by Dr. A. G. Böving. They agree closely with the description of *Triodonta* (*Serica*) *aquila* Cast. by Perris (1877, p. 116). The labrum is more symmetrical than in most of the Melolonthinae and has its distal lobe rather strongly produced. The lateral lobes are margined on the inner aspect by the series of lateral striae. The margins of all three lobes are provided with rather numerous setae, which increase in length distally. There are three prominent spines in the distal sensory area, but no sensillia have been found. Close study may probably show that they are present. The surface of the epipharynx is covered with small setae except for a cleared central space. The tormae are unequal in size and dissimilar in shape. The right torma reaches almost to the median line, and at its end is located the conspicuous sense-cone of the proximal sensory area.

Tribe Melolonthini.—*Diplotaxis* sp. is described from a first instar larva (Fig. 34). The epipharynx is broadly oval, with only the distal end bearing setae, about eight in all. The ental surface bears a small patch of comparatively long setae, which are directed meso-distad. They meet on the meson and overlap each other. Between these and the distal margin are a few short, broad setae. The lateral margins lack the series of lateral striae which occur in other Melolonthinae and also in the tribe Anomalini. The distal sensory area is located at the base of four spines with apices directed proximad. Five sensillia can be distinguished at the base of these spines. An irregular series of short setae extends from these spines to the clypeal area. The tormae are poorly developed, the left one being more heavily chitinized than the right, which is almost obsolete. In the area of the epipharynx, distad of the right torma, is a darkened, narrowly chitinized area, which extends disto-proximad. This may be a structure that is not normally present. A small dark area distad of the left torma is probably a sense-cone of the proximal sensory area.

The labrum of *Phyllophaga futilis* (Lec.) (Fig. 37) is asymmetrical, and its distal margin is extended to form a lobe which is covered with a mass of long, slender, articulate setae. The lateral margins are rounded and bear on each side about 16 broad and rather strongly curved, articulate setae. Near the base of each of these setae on the ental aspect is a narrow ridge, or carina, extending toward the meson. This series of carinae give each margin a file-like aspect. They are the lateral striae. Immediately behind the distal lobe and slightly laterad of the meson is another series of ridges, about nine in number. The individual ridges extend nearly disto-caudad, while the series taken as a whole lies obliquely. These are the submarginal striae. Immediately mesad of the submarginal striae on the right (left in sketches) is a darkened, more heavily chitinized area—the distal sensory area. Near

the meson and slightly in front of the middle is a group of six strong spines pointing proximally and having their bases arranged in almost a semi-circle. Three or four other spines of the same nature are situated caudad of the semi-circular group of six. These spines are distinguishable from the neighboring setae by their larger size and the fact that they are not articulate at the base. Distad of the spines and located near their base is a group of pore-like sense-cones arranged somewhat semi-circularly but irregular as to their distance apart. There are six comparatively large cones and five smaller ones alternating with them about the semi-circle. Proximad of the series of spines and sense-cones in the distal sensory area is a large number of articulate, recumbent setae whose apices are directed mesad and mesocaudad. They likewise are semi-circularly arranged, leaving an area in the center with no setae. The series extends to the tormae on the proximal margin of the labrum. On the left of the clear central area (right in sketch), near the proximal margin, is a cluster of long, slender, fixed spines. These lie in part between the branched arms of the left torma. The tormae, located on the clypeo-labral suture, are long, irregular, and asymmetrical. The right torma extends almost to the meson and is unbranched; while the left torma is shorter and is two-branched near its mesal end, with one of the branches, long and slender, extending far onto the labrum. At the mesal end of the left torma is another clump of fixed, slender spines, and mesad of these are about 25 clypeal sensillia. Between these sensillia and the end of the right torma, slightly off the median line, is a triangular chitinous area, almost spine-like, called the chitinous plate by Ritterschaus. It is directed mesodistad. Immediately mesad of the chitinous plate, and apparently partly underlying it, is a broader, less heavily chitinous area pointing in the same direction and covered with long, slender spines (Fig. 69). In cleared specimens, four sense-cones are apparent, which are intermediate between the sensillum ampullaceum and sensillum coeloconium types. Each of these consists of a sunken, fungiform cone which connects with a long, somewhat bottle-shaped canal. The central structure containing the sense-cone is called the "sense-cone" by Ritterschaus. The ental surface of the clypeus, upon which we find the chitinous plate and the area bearing the sense-cones, is called the "epigusta" by some writers (MacGillivray, *et al.*). Just behind the sensory area is a long, transverse, strongly bowed, chitinous bar. All of the structures between the tormae comprise the proximal sensory area.

The epipharynx of *Phyllophaga lanceolata* (Say) (Fig. 26) differs in some detail from the common epipharyngeal form found in this genus, the most conspicuous differences being a more nearly symmetrical outline of the labrum and the presence of only four prominent spines in the distal sensory area. A closely allied species, *P. cribrata* (Fig. 35), is of the typical form, including the usual number of spines on the distal sensory area. Another

species, *P. tristis* (Fig. 27), differs in having but three prominent spines in the distal sensory area.

In the genus *Polyphylla* (Fig. 25), which also belongs to the tribe Melolonthini, the characters are quite similar to those of *Phyllophaga* except for a somewhat different arrangement of the spines on the distal sensory area. The lateral striae are also shorter and less distinct.

Tribe Macrodactylini.—The epipharynx of *Macrodactylus subspinosus* (Fab.) (Fig. 28) is described from specimens in the Davis collection of the U. S. National Museum. The labrum is asymmetrical, with a single emargination of the distal margin slightly to the right of the median line. The margins, both lateral and distal, are provided with intermixed long and short setae. Lateral striae are present on the inner surface of the lateral margins. Beginning at the notch, or distal emargination, is a more darkly chitinized, irregular plate, which extends proximad to the distal sensory area. In this area is a group of pore-like sensillia arranged in an irregular semicircle. Some of the sensillia are arranged in pairs. From this same area four strong spines are directed toward the clypeo-labral suture. Between the distal sensory area and the clypeo-labral suture a number of setae are arranged in a circle with a non-setose area in the center. The tormae are unequal in size, the left one being considerably smaller than the right. At the end of the left torma is a prominent row of slender, elongate spines. The right torma extends nearly to the median line where the sense-cone of the proximal sensory area is located. In some specimens the cone is a single tooth-like structure, while in others it appears as two teeth (Fig. 28).

Rutelinae

Tribe Anomalini.—The epipharynx of *Popillia japonica* Newm. is quite similar to other species in the tribe. Its close relationship to the Melolonthinae is shown by the presence of the lateral striae, which occur only in these two groups, and by the resemblance in the form and arrangement of the sensory area including the spines, which, however, are fewer in number than in the Melolonthinae. The following species were available for study: *Popillia japonica* (Fig. 41), *Strigoderma arboricola* (Fig. 52), *Anomala orientalis* (Fig. 40), *A. kansana* (Fig. 43), *A. binotata* (Fig. 49), and *A. innuba* (Fig. 46). Except for some variation in the number and arrangement of the spines of the various species, they exhibit rather marked uniformity in structure. The same can be said of *Anomala phyllopertha*, which has recently been described by Ritterschaus (1927). Böving (1921) has figured the epipharynx of *Popillia japonica* but has not given a detailed description of its structure. The labrum (Fig. 41) is strongly asymmetrical, as in the others studied in this tribe except *Anomala orientalis*, which is nearly symmetrical. The distal margin is usually produced into an acute lobe covered with rather long setae. The lateral margins are strongly rounded

and bordered with short, curved setae, at the bases of which are to be found the lateral striae, and with a few extremely long setae intermixed. The distal sensory area has three strong spines and two large articulate setae which might be confused with the fixed spines. At the bases of the fixed spines there are about eight sensillia arranged in a curved line. Between the distal sensory area and the clypeo-labral suture numerous smaller setae are circularly arranged with the customary, smooth, non-setaceous, central area. The tormae are of nearly equal size and do not reach the median line. At the mesal end of the right torma a pointed, chitinous plate and a tubercle-like sense-cone comprise the proximal sensory area. Two pore-like clypeal sensillia are to be found in the cleared area mesad of the sense-cone and proximad of the distal end of the left torma. Latero-proximad of these pores are a number of minute spinules only noticeable under high magnification.

Tribe Rutelini.—Three species of this tribe were studied. They differ strikingly from the tribe Anomalini of the same subfamily and exhibit affinities toward the Dynastinae. *Polymoechus brevipes* Lec. (Fig. 47) is decidedly irregular in outline; *Pelidnota punctata* (L.) (Fig. 44) is more regular and is wider than long; while *Cotalpa lanigera* (L.) (Fig. 50) is longer than wide. The arrangement of the distal sensory area is sometimes hard to make out. It varies more markedly than in the Anomalini. In *Cotalpa* the general form is only slightly asymmetrical, the sides are gradually rounded and no prominent lobes or emarginations are formed. The lateral margins are covered with curved setae which are comparatively short in the proximal region but become longer distally. No lateral striae are present. The distal sensory area is composed of a single chitinous structure produced into a point resembling a spine. Proximad of this structure are a few strong, spine-like, articulated setae. They are directed toward the clypeus, while the remaining setae covering the epipharynx are directed toward the meson with a smooth area in the middle. The tormae are irregular, the left one being curved distad while the right lies transversely. A fold in the integument at the mesal end of the left torma makes this torma appear much longer than it is. At the end of the right torma is the proximal sensory area, composed of a minute, triangular, chitinous plate and a broadly rounded sense-cone.

Dynastinae

Tribe Cyclocephalini.—The epipharynx of *Ochrosidia immaculata* (Oliv.) (Fig. 53) is characterized by the absence of lateral striae along the ental surface of the lateral margins and by the presence of two broad chitinous spines in the distal sensory area. The right spine is nearly twice as broad as the left, and its apex is more rounded. In cleared specimens three sense-cones can be distinguished in this spine. The left spine is more pointed and has at least one sense-cone in it. The lateral margins of the labrum are

comparatively smooth and strongly rounded. They bear about 14 broad and strongly curved setae pointing distally, each of which is slightly longer than the preceding one. The distal margin is more rugose and is armed with a group of long setae. Between this group of setae and the spines described above there is a small, narrow, somewhat curved, chitinous plate, or ridge, which lies obliquely. There are two sense-cones located in the space between this chitinous structure and the two broad spines. A large series of setae of various sizes lie between the spines and the clypeo-labral suture. The setae are inclined in all directions and are so arranged as to leave a cleared area in their center.

The tormae are comparatively short and decidedly asymmetrical. The torma on the left is at first directed proximad, but it soon makes a prominent bend and narrows down toward its extremity, which is near the clypeo-labral suture. The right torma is at first curved proximad but has a less conspicuous curve, so that it extends in an almost transverse direction. At its distal end in the proximal sensory area on the clypeus are two chitinous processes pointing distally. The one almost abutting the end of the torma, and slightly overlapping it, is the larger. This is the chitinous plate. No sensillia were noted in it, but the smaller process which is the sense-cone shows one sensillum. Scattered throughout the large central group of setae are a number of very small dots which are circular in outline and exhibit within them another concentric circle. These are doubtless pore-like sensillia.

Representatives of three other of the five North American tribes of this subfamily have been studied—*Ligyrodes (Ligyryus) relictus* (Say) (Fig. 42) and *Ligyryus gibbosus* DeGeer (Fig. 45) of the Pentodontini, *Strategus antaeus* (Fab.) (Fig. 48) of the Oryctini, and *Dynastes tityrus* (L.) (Fig. 54) of the Dynastini. They differ from *Ochrosidia immaculata* principally in that the chitinous portion of the distal sensory area is produced into a single point, except in *Dynastes* which has two projections located much closer to the margin and much larger proportionally than in *Ochrosidia*.

Cetoniinae

Tribe Gymnetini.—The Cetoniinae are characterized by having the labrum symmetrical and usually biemarginate and trilobed. The distal sensory area is composed of a group of comparatively short, strongly curved setae which are stouter than the remaining setae. In a few species (*Osmoderma et al.*) these setae are apparently not articulate and, as such, are considered as spines.

In *Cotinis nitida* (L.) (Fig. 59) the labrum is deeply biemarginate on its ectal surface but not strongly so on the ental aspect. The trilobed condition of the epipharynx, therefore, is not strongly marked. The lateral lobes have a few short setae, which become more numerous and longer distally. The

median lobe has only a few long setae. It is marked off internally on its lateral areas by a darkly chitinized band extending on each side from the margin to the distal sensory area. Between these bands and at the base of the circular row of setae are two pore-like sensillia. The circular row is composed of about 15 setae, and proximad of these are other setae of similar size. The remaining surface of the epipharynx is covered with longer and more slender setae which become shorter laterally. There is left on the central disk a comparatively small area devoid of setae. The tormae are shorter than in most groups, and the right one is a little longer than the left. Between them in the distal sensory area is a single large sense-cone. The chitinous plate of this area is absent. Some distance proximad of this sense-cone are two pore-like clypeal sensillia.

Among the other species studied in this subfamily, *Trichiotinus piger* (Fab.) (Fig. 66) is the only one that differs radically from others of the group. It was studied in a first instar larva. It does not show the trilobed feature, nor is the circular row of setae in the distal sensory area as marked. *Cremastocheilus* sp. (Fig. 65) was studied from a cast skin in which the epipharynx is nearly devoid of setae, apparently because they were rubbed off, since numerous trichopores are present having the characteristic arrangement of the group. A single sense-cone is present in the proximal sensory area. Three species of *Euphoria* (Fig. 57, 60, 63) are markedly similar, while *Stephanucha philipennis* Kr. (Fig. 68) appears to lack the sense-cone of the proximal sensory area and has the setae of the distal sensory area more obliquely curved.

Trogidae

This subfamily of Scarabaeidae has recently been raised to family rank. Tillyard (1926) has pointed out in his book, "Insects of Australia and New Zealand," that the Trogidae are intermediate between the Scarabaeidae and Lucanidae. This is also apparent in the larvae in the condition of the stridulating apparatus of the meso- and metathoracic legs and the feebly trilobed anal area, which suggest relationships to the Lucanidae.

The epipharynx of *Trox* sp. (Fig. 39) is symmetrical and neither trilobed nor emarginate. Its lateral margins are almost devoid of setae except distally where five or six large setae are continuous with those of the distal margin. The median distal margin is produced into four conspicuous tubercles, each of which bears a strong seta. The distal sensory area is indistinct, and in the specimens examined its detail is hard to distinguish. Only a few setae are scattered over the lateral lobes, about four on each lobe. The central area is darkened in the specimens, and no detail can be made out. The tormae are small, the right one being the larger. No detail of, or evidence of, a proximal sensory area is apparent.

Lucanidae

The subfamily Dorcinae (Fig. 30), represented in the University of Illinois collection by some larvae labeled *Dorcus* sp. with no other data, lacks the prominent circle of spines found in *Sinodendron* and is more setaceous both on its distal margin and its ental surface. The distal lobes are not so strongly evident, the emarginations being not so marked. The distal margin is densely setaceous, but the lateral margins are nearly bare of setae. The general shape of the labrum is much like *Sinodendron*, being somewhat subquadrate. The entire ental surface is sparsely set with short setae interspersed with small pores which may be sensillia but also may be the tri-chopores, or alveoli, of setae which have been broken. No circular area of spines is present, but near the middle of one specimen is a semi-circular depression which does not appear to be a normal structure. The tormae are strongly curved at the lateral margin. They extend transversely mesad to unite on the middle line, where another chitinous process projects distad along the mesal line a little more than one-third the distance of the labrum. Behind the fused tormae is a long, narrow sense-cone which is somewhat rounded distally and which ends caudally in three parts. Three, small, cleared areas near its distal end may be sensillia. On the left side of this structure is a much smaller, more transparent, chitinous plate, the distal end of which is rounded. On the right side of the sense-cone is a much larger, backward-pointing, chitinous plate which ends in a sharp point. No trace of sense-cones is evident in these lateral processes.

Aesalinae.—The general shape of the labrum of *Sinodendron rugosum* Mann (Fig. 33) is subquadrate. Its lateral margins are smooth, non-setose, and slightly divergent toward the distal end, where they round off to form the distal margin, which is slightly three-lobed, the lobing being produced by two emarginations, one on each side of the meson. The central lobe bears four setae on its margin and two others that are submarginal. Each of these setae arise from a small papilla. On the ental surface the median lobe is rather strongly convex. On the left of the meson behind the setae is a slight, chitinous spine which is frequently hard to find. Overlapping the median lobe and extending to the clypeo-labral suture is a prominent, almost circular row of spines enclosing a slightly depressed, smooth area. The lateral lobes of the distal margin bear five or six setae, in one specimen five, on the right lobe and six on the left lobe. The rest of the epipharynx is smooth. The tormae are stout on the lateral margins. A pointed process extends meso-distally while another transverse process meets a similar one from the other side to fuse mesally where a pointed projection extends distally along the meson into the clear area surrounded by the circle spines. On the clypeus, proximad of the central chitinated process of the tormae, are two chitinated plates somewhat setaceous on their distal ends, and between these is a long tooth-like process. No sensillia, as found in

Phyllophaga, can be made out in these processes even with the oil-immersion lens. The setaceous distal ends of the lateral plates are probably sensory, while the central process shows under high power a clear central area that may be thinner and may serve in a sensory capacity.

Passalidae

The epipharynx of *Passalus cornutus* Fab. (Fig. 36) is trilobed and nearly symmetrical. The lateral lobes are clothed with a mixture of long and short setae, but the median lobe has only seven setae on its margin and is bare of setae on the ental aspect nearly to the middle of the epipharynx, where there are two rather well defined curved rows of short setae, with their apices directed distally—not as in the epipharynx of other species studied—and laterad of these rows are a number of long setae with their tips directed mesally. No sensillia have been found, but closer study of the distal margin of the median lobe may reveal their presence. The tormae are unequal in size, the left being the larger. They are comparatively small. The present description is made from the specimen shown in Figure 3. Other specimens show the setae of the median area to be arranged somewhat differently.

MANDIBLES

The mandibles (Fig. 70 to 89) are strongly chitinized and somewhat longer than wide. The distal area is usually much darker than the proximal area, which is generally of the same color as the head. A given species may exhibit a marked difference in the shape of the right and left mandible. Perris (1877, p. 93) points out that they are usually provided with teeth, having two teeth on the right mandible and three on the left as a rule. The mandibles exhibit two distinct regions, a proximal and a distal area. Böving (1921) has termed the proximal region the manducatorial region, or the grinding area (also called the molar area, Fig. 81, *mo*), and the distal part the scissorial region (*sc*), or cutting area. The molar area of the left mandible is, as a rule, larger than that of the right mandible. Behind the molar area is a thinly chitinous, setaceous area, the acia (*ac*). This appears to arise on the ventral aspect, where it can be observed that the right acia is long and pointed while the left one is shorter and more rounded. On the dorsal aspect (Fig. 70) is the acetabulum, or preartis (*pa*), by which the mandible articulates with the condyle, or precoila, at the ends of the fronto-clypeal suture. An enlarged sketch of this articulation is shown in Figure 77, in which the preartis is seen to articulate with a condylar precoila (*pcl*). The lateral aspect of each mandible presents a flattened surface, or scrobe (*sb*), bearing a few setae.

The cephalic or anterior surface of the mandibles (Fig. 70 to 80) presents, on the whole, a convex contour, and in all but *Canthon laevis* and a few others it shows two distinct regions limited by a ridge, which is represented

by the dotted lines in the drawings. This ridge, and in most cases a change of contour, indicates the areas covered and uncovered by the labrum when the mandibles are in repose.

The caudal surface of the mandibles (Fig. 81 to 89) presents the notched aspect of the scissorial area (*sc*) in much the same manner as the cephalic aspect but possesses in some species a transversely striated area (*sa*) in the form of an oval. This is part of a so-called stridulating apparatus which occurs in a number of scarabaeid larvae and has been described by Schiödte (1874) and others. Opposed to this series of transverse striations on the maxillae is a variable number of stridulating teeth (Fig. 97, 113, 106 *ms*) which will be described in connection with the maxillae.

On the caudal aspect of the molar area can be noted the *acia* (*ac*), described above, and in addition, on the right mandible (Fig. 81), a somewhat rounded, lobe-like structure which is apparently absent on the opposite mandible and which overlaps the hypopharynx when the mandible is closed. This lobe plays an important role in the grinding of food. It will be mentioned later in connection with the hypopharynx. This aspect presents a condylar articulation, the postartis (*pta*), on each mandible, which articulates, as seen in Fig. 109, with an acetabular postcoila (*ptc*) located on the gena. Attached to each mandible, but shown in only a few sketches (Fig. 70, 81, 89), are two chitinous processes for the attachment of muscles, which have been described as tendons. The mesal tendon has been termed the rectotendon (*rt*) and the lateral one the extensotendon (*et*). The right mandible of *Canthon laevis* (Fig. 78, 85) has the scissorial area prolonged into a narrow blade with no emarginations forming teeth. The left mandible (Fig. 78, 85) has the regions notched to form three strong and quite distinct teeth, and the manducatorial area has a single tooth larger than the others and truncate at the end. The same area on the right mandible lacks the tooth, but the whole is produced into a convex grinding area that fits into the concave grinding area of the left mandible. This species bears a series of small rugosities in place of the ovate series of transverse, stridulating striae.

The shape of the mandibles in *Canthon ebenus* is not the same as in *C. laevis*. The right mandible has two teeth, and the left has three, on the scissorial area. *Onthophagus pennsylvanicus* seems to resemble *C. laevis* more closely. The right mandible has a long narrow scissorial tooth, while the left has three, and the manducatorial area has one large truncate tooth. The scissorial area of the right mandible of *Phyllophaga crassissima* (Fig. 76, 84) is a long blade-like structure devoid of any notches producing teeth. The manducatorial area is comparatively small, compared to that of the left, and is somewhat concave when viewed on the dorsal aspect. The scissorial area of the left mandible (Fig. 76, 84) is stouter than the right and from the dorsal aspect presents, on the inner side, an irregular margin

scarcely strong enough to be called toothed. When viewed from the ventral side, there appear two rather prominent teeth on the cutting edge. The grinding area is much stouter on the left and bears near its base a strong tooth. *Phyllophaga lanceolata* differs from *P. crassissima* in having a prominent tooth on the scissorial area of the right mandible and two somewhat less conspicuous teeth on the left. The same difference in size of the molar area is here noted as in *P. crassissima*. As in the Coprinae, the transverse, stridulating striae are replaced by a slightly rugose surface.

In *Diplotaxis* the right scissorial area is long and blade-like with a single prominent tooth, and the manducatorial area is small, compared to that of the scissorial region. The scissorial area of the left mandible is proportionately more slender and ends in a sharp point. There are two conspicuous teeth on the inner edge, and the manducatorial region is produced to form a rather noticeable tooth near its cephalic margin. The scissorial and molar areas of *Cotalpa lanigera* (Fig. 74, 83) are proportionately much stouter than in the species of the Melolonthinae studied. The right scissorial area has a serrated inner edge, and the tip end is broadly obtuse. The grinding area is somewhat smaller in the left mandible and bears three conspicuously elevated grinding surfaces. The scissorial region of the left mandible has a small tooth on the cutting edge, which is rather sharp, and the molar surface presents quite an irregular margin, thus differing somewhat from the right mandible.

In *Polymoechus brevipes* the scissorial region is quite similar in both mandibles. The area ends in a rather sharp point, near the tip of which there is a single sharp tooth. The molar areas are of approximately the same size on both mandibles, but one is slightly concave to fit the convexity of the other. The right scissorial area of *Anomala binotata* is comparatively smooth on the inner edge, no teeth being present, and the structure has a rather truncate termination. The left mandible is likewise truncate, but its cutting edge bears two teeth, one rather obtuse and the other acute. The right molar surface is rather flat and smooth and about the same size as the left. In *Anomala aenea*, figured by Schiödt, both the scissorial areas end acutely and the inner cutting edges each bear a single tooth. All Rutelinae studied have an ovate series of transverse stridulating striae. The mandibles of *Ligyris gibbosus* (Fig. 75, 88) are quite dissimilar in shape. The right scissorial area has a smooth cutting edge and is truncate on the end. The left is rounded at the tip, and the cutting edge bears three rather obtuse teeth. The grinding regions are approximately the same size, but the left bears a tooth, as in *Phyllophaga crassissima*, which is lacking on the right molar surface. *Ligyroides relictus* has two obtuse teeth on the cutting edge of the mandible. The right is truncate and the left is broadly rounded as in *L. gibbosus*. Likewise the grinding areas are similar to those of *L. gibbosus*, and the whole mandible is proportionately broader and stouter. The man-

dibles of *Ochrosidia immaculata* are acutely pointed and more slender, and the cutting edge of the left bears two teeth, one of which is obtuse and the other acute, while the grinding surface has numerous teeth with an especially large one at the cephalic margin. The right scissorial area is acutely pointed, and the inner edge has one conspicuous tooth that is obtusely pointed. This subfamily has the transverse stridulating striae on the caudal aspect. The mandibles of *Euphoria inda* (Fig. 73, 82) are proportionately shorter than in the other groups except the Coprinae. The right scissorial region is notched at the end, giving the appearance of a broadly truncated tooth and a small, somewhat acute tooth. The molar area is larger than the cutting region. It is slightly concave and has two teeth. The left scissorial area is truncate at the end and has two large teeth on the cutting edge, while the manducatorial area is convex and bears three broad, short, grinding teeth. All Cetoniinae, as far as known, have an oval stridulating area on the caudal aspect. In the specimens studied of the genus *Trox* (probably *T. unistriatus* Beauv.), the mandibles do not differ strikingly from those of other genera previously described. The stridulating area on the caudal surface is not present. The scissorial area of the right mandible presents a long terminal tooth and another formed by a small notch on the mesal margin. The molar area on this mandible consists of one large, broad tooth and a smaller, but longer, isolated tooth distad of the larger one. The scrobe bears a conspicuous ridge, or carina. The left mandible is quite similar in the scissorial area, and the molar area differs but little in size. Practically the entire structure is very darkly colored. In *Sinodendron rugosum* Mann (Fig. 80) the mandibles are entirely black in color. They are, as in the others, asymmetrical. The distal end of the scissorial area of the left mandible bears three teeth, which are nearly subequal, while the right has but two, of which the terminal one is longer and more slender than the adjacent one. The molar area of the left mandible is larger than that on the right. The stridulating area is absent. In *Ceruchus piceus* (Web.) the dentation of the scissorial area is similar to *Sinodendron*, and the opposing molar areas are dissimilar in shape and size. Specimens of the genus *Dorcus* show no striking differences from *Ceruchus* and *Sinodendron*. In both *Ceruchus* and *Dorcus* no stridulating area is present on the caudal aspect. Perris (1877, pl. 5, fig. 157) shows a right mandible of *Lucanus* with three terminal teeth and no stridulating surface, thus corresponding to the genera here described. The mandibles of *Passalus cornutus* differ considerably from those of the Lucanidae (Fig. 79, 89). The terminal teeth of the scissorial area are three in number on both mandibles, and the molar area is nearly similar on both. It consists of a broad, cup-like tooth, which is strongly depressed on the mesal aspect. Both more nearly approach each other in symmetry than in any other members of the superfamily. The stridulating surface on the caudal aspect is lacking.

MAXILLAE

The maxillae (Fig. 97 to 100 and 103 to 104) present the usual number of parts found in a chewing type except that the galea and lacinia may or may not be fused to form the single structure known as the mala (*m*). The cardo (*cd*) articulates with the postgena (*eg*) (Fig. 109) by an articular acetabulum, the parartis (*pra*), which fits into the paracoila (*prc*) located on the postgena. There are two divisions of the cardo, a subcardo (*sc*) which bears the articulation and an alacardo (*ac*) lying between the subcardo and the stipes. The stipes (*s*) is quadrilateral in outline on the caudal aspect, except at its distal end where it is fused to the mala, while on the cephalic aspect it is not separated from the mala. The palpifer (*pf*) is borne on the dorso-lateral margin of the stipes. On the mesal margin is a narrowly elongate sclerite, the parastipes (*ps*), or subgalea of many authors. A membrane termed the labacoria (*lc*) by MacGillivray (1923) is attached to the inner margin of the cardo, parastipes, and stipes. This membrane attaches to the labium and helps close the oral aperture. The mala (*m*) is densely setaceous and distally bears a series of strong spines (Fig. 115 to 117). In many larvae of the coprophagous Scarabaeidae, all the Lucanidae, Passalidae, and Trogidae, the lacinia and galea are distinctly separate and show no traces of fusion. The series of teeth-like structures found on the cephalic aspect are variable in number (Fig. 111 to 114 and 118, 119, 124, 125), there being usually more on the right than on the left maxilla (Fig. 112). These teeth may point and curve toward the distal extremity of the stipes or may be short, blunt, and not curved (Fig. 113, 118). They usually lie in opposition to the oval, file-like area on the mandible (Fig. 81, 88). These stridulating structures, if such they be, have been described by Schiödt (1874), who asserts that the teeth of the maxillae differ in number and form according to the genera, and further notes that they vary in number from five to twenty, sometimes being straight but more often being extremely sharp and curved. The maxillary palpi (*mp*) are three- or four-segmented.

The cephalic aspect of the maxillae (Fig. 97 to 100, 103, 104) is slightly different from the ventral aspect and will, therefore, be described separately. The cardo is large and subquadrate in all the genera figured. The stipes is limited by a suture from the cardo and may, or may not, be differentiated from the galea, while on the ventral surface there usually appears a suture separating the stipes and galea. The maxillary lobes (galea and lacinia) are separate or bifid in some of the genera, while in others there is a deep longitudinal sulcus which is the limiting line between the two parts.

In the Coprinae (*Canthon laevis*, Fig. 98) the cardo is subquadrate and has a longitudinal suture dividing it into a larger and a smaller area. The stipes likewise is subquadrate and bears on its mesal margin the lacinia which terminates in a single, strong tooth (Fig. 117). On the latero-anterior

margin of the stipes is a smaller sclerite, probably the palpifer or a portion of the galea, from which is articulated the maxillary palpus. Distad of the palpifer is the lobe-like galea which is rounded at the end and bears numerous setae. *Canthon ebenus* also has the two regions, galea and lacinia, separated. The same is true of *Aphodius* (Fig. 100), *Onthophagus pennsylvanicus*, all the Lucanidae, Trogidae, and Passalidae (Fig. 103).

The Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae present much the same appearance dorsally and will not be described separately. In each the cardo is subquadrate; the stipes and galeae are not separated; and the two lobes, galea and lacinia, are fused but are limited on the dorsum by a distinct suture. On the dorsum of the stipes are the stridulating teeth which lie opposite the stridulating areas of the mandibles. Concerning these Schiödt (1874) says:

"Les dents de la tige des mandibules servant à râcler les granulations mandibulaires diffèrent de nombre et de forme selon les genres: il y en a de six jusqu'à vingt et au delà; quelquefois elles sont droites et trèsfortes, mais le plus souvent elles sont extrêmement aiguës et recourbées en crochet."

In *Canthon laevis* (Fig. 119) there are six, large, pointed teeth and a number of very minute teeth immediately cephalad of the larger ones. *Phyllophaga crassissima* (Fig. 118) has fourteen rather blunt or quadrate teeth; *Ligyryus gibbosus* (Fig. 124) has thirteen; *Euphoria inda* (Fig. 125) has six, which are long and pointed; while in *Cotalpa lanigera* (Fig. 114) only five rather blunt teeth are found. These teeth have been observed only in the Scarabaeidae.

On the caudal aspect the important differences from those of the cephalic are the sharp delineation of the stipes from the galea, the absence of the longitudinal sulcus marking the fusion of the galea and lacinia, and a few indistinct sutures dividing the cardo into a number of irregular areas. The galea and lacinia of *Canthon laevis* and others with a bifid mala are separate as on the cephalic aspect, while the two are completely fused in other groups. The palpifer is distinctly evident in most species.

The spines and setae found on the galea and lacinia are shown from the mesal aspect in Figures 115, 116, 117, 120, and 121. Upon closer study these may prove of decided taxonomic value. The stronger spines are termed *unci* (singular-*uncus*) by Böving (1921).

Canthon laevis (Fig. 117) has on the terminal end of the lacinia a single uncus. On the fused lobes of *Phyllophaga crassissima* (Fig. 121), there are three rows of unci, with four to six teeth per row. *Ligyryus gibbosus* (Fig. 115) has a single terminal uncus and two others standing close together. *Euphoria inda* (Fig. 120) has one terminal and five mesal unci and a number of strong setae.

The fusion of the galea and lacinia seems to be typical of the higher Scarabaeidae. On the dorsal surface of the maxillae there remain traces of

this fusion indicated by the longitudinal sulcus. This condition may be correlated with the food habits. The families Trogidae, Lucanidae, and Passalidae (Fig. 103) all resemble the coprophagous Scarabaeidae in having the galea and lacinia separated.

HYPOPHARYNX

The hypopharynx consists of a densely setaceous area on the ental aspect of the fused glossae and paraglossae and a strongly chitinized area (Fig. 128 to 132), termed by Böving (*loc. cit.*) the hypopharyngeal chitinization (*hc*). The hypopharyngeal chitinization (Fig. 134) is decidedly asymmetrical and somewhat less densely chitinized on the lateral extremities where it is irregularly inflexed to fit snugly against the molar region of the mandibles (Fig. 133) and, in the opinion of the writer, serves as an accessory organ of mastication. The caudal margin of the chitinized area is continuous with the pharynx (Fig. 134), which is probably held open by rod-like structures extending dorsally to the epipharynx. In one preparation it was noticed that there is a direct connection between the ental aspect of the clypeus and the hypopharynx. These connecting bands, of what appear to be slightly chitinized membranes, are shown in Figure 91, extending between the clypeus (*cl*) and the hypopharynx (*hc*). On the dorsal aspect, near the lateral angles, is a series of small setae which are similar to the structures described by Carpenter (1912) as the maxillulae which Crampton asserts are homologous to the crustacean paragnatha.

The hypopharynx consists also of a series of thickly set spines located on the glossa. They vary considerably in the genera studied. Immediately behind the setae is the heavily chitinized, asymmetrical hypopharyngeal chitinization (Fig. 134). The setae of the hypopharynx of *Canthon laevis* (Fig. 130) are arranged in the form of a semicircle and seem in this respect to differ entirely from the other genera studied. In *Phyllophaga crassissima* (Fig. 131) and *Ligyris gibbosus* (Fig. 132) the setae are arranged in a circular group, with their points directed toward the center. In *Cotalpa lanigera* (Fig. 128) they are arranged in a triangle, and most of them are pointed distally. In *Euphoria inda* (Fig. 129) there is a double longitudinal series, one within the other, of setae which tend to converge distally and which point toward the median line.

The hypopharyngeal chitinization of the higher Scarabaeidae is quite similar (Fig. 128 to 134). *Canthon laevis* (Fig. 130) differs markedly. It appears to have the chitinized area divided into two irregular structures both of which are more heavily chitinized on the right side. The structure in the other four genera figured is obliquely transverse and has the right side produced into a more or less blunt end which is more heavily chitinized. The hypopharynx of the families other than the Scarabaeidae has not been carefully studied. In the Passalidae and Trogidae it is more simple, not

being as heavily chitinized, while in the Lucanidae this structure is more pronounced and approaches the higher Scarabaeidae in degree of development. Further study of the hypopharynx may reveal characters of taxonomic value in these structures.

LABIUM

The labium (Fig. 92) is small and usually concealed. It is partly covered on its lateral margins by the maxillae. The submentum (*sm*) is large and somewhat quadrate. It is bordered laterally by the maxillae (*mx*). A smaller, narrow, transverse area represents the mentum (*mt*) which is sharply differentiated from a wider transverse, stipula (*st*). Laterally, the stipula may be prolonged into a deflexed, broadened lobe which is covered by the maxilla. The stipula is broadly rounded on the distal margin. It is strongly setose and bears a pair of small, two-segmented labial palpi (*lp*). Since the labia of the various genera differ from each other less than any other structures of the mouthparts, they are not given extended consideration, although the shape of the various parts differs somewhat, as do also their size and proportion.

THORAX AND ABDOMEN

SEGMENTATION

The thorax (Fig. 1 to 12) consists of the usual three segments, each of which, except in the Passalidae, bears a well-developed pair of jointed legs. The Passalidae have but two pairs of well-developed legs on the pro- and mesothorax and a greatly reduced pair of metathoracic legs. The prothorax (Fig. 8, *I*) may (Fig. 12), or may not (Fig. 1 and 3), be divided dorsally into two or three annulets. The division of the cephalic annulets usually does not extend onto the pleuron. Sometimes a small area of the cervix lying in front of the cephalic annulet is apparent, depending on the degree of extension or retraction of the head. This may cause the prothoracic segment to appear broken up dorsally into four annulets. The cephalo-ventral angle of the propleuron frequently extends forward to partially overlap the head capsule. The propleuron in some forms (Trox, Fig. 7) is more deeply pigmented and slightly more heavily chitinized.

The meso- and metathorax in Passalidae are similar to the prothorax in not being divided into annulets. In all other species noted there are two or three annulets present. In *Pinotus* (Fig. 1) but two annulets occur, while many show three distinct divisions. Perris (1877, p. 94) wrote that the meso- and metathorax, in those species with annulets, were equally divided by a single fold and that the largest division was anterior in the mesothorax and posterior in the metathorax.

The number of abdominal segments is variously counted as nine by some workers (Perris, 1877) and ten by others (Böving, 1921). In *Passalus*

(Fig. 3) there are ten distinctly evident segments, and in many others (*Anomala*, Fig. 8) ten can be easily discerned. Some genera such as *Aphodius* (Fig. 6) and *Euphoria* (Fig. 11) show a tendency towards a coalescence of the ninth and tenth segments. The first eight segments of *Passalus* show a slight diagonal depression tending towards the formation of a small anterior and a large posterior annulet. The *Lucanidae* (Fig. 2) and some of the *Scarabaeidae* (Fig. 1, 4) show but slight annulations. The first six or seven segments of the more common *Scarabaeidae* are thrown into deep folds, forming usually three distinct annulets. The caudal segments are not so constricted. The integument appears stretched and often is partly transparent. The last segment has been called the "sac" by Erichson (1848), which is a term that is used by some European workers to designate the region of the abdomen behind the last spiracle-bearing segment. The sac on its dorsal surface is usually divided by a transversely impressed line which gives in many groups the appearance of two body segments behind the last spiracle-bearing segment. The *Cetoniinae* lack this transverse impression and appear as having but a single segment behind the segment which bears the posterior spiracle.

SETATION

The *Passalidae*, *Lucanidae*, and some *Scarabaeidae*, such as *Pinotus*, are sparsely provided with setae scattered over the body. They are usually lacking in short, stiff spines, except on the ventral part of the last abdominal segment. Most of the *Scarabaeidae* have in addition to the scattered setae a varying number of rows of short, stiff spines that are more noticeable on the dorsal annulets of the anterior body segments and become less dense on the posterior segments. *Amphicoma* (Fig. 139) is especially densely setaceous, and all degrees occur between its condition and that of *Passalus*. The setation of the last ventral segment presents a wide difference in the arrangement of the various spines and setae (Fig. 138 to 191), which have been made use of in the keys in the taxonomic section of this work. These will be described under the term "radula." Arrow (1910, p. 11) points out that the spines on the body aid in progression "and probably also render the grub a less agreeable article of food." It is well known that many *Cetoniinae* do not use their legs but crawl on their backs, and in this they are aided by the dorsal spines.

RADULA

The radula (Fig. 138 to 191) is the rake made up of the spinose and setose area located on the ventral aspect of the last abdominal segment. The function of this structure was described by the writer (1927) as serving as a rake to clean the mouthparts. Ritterschaus in a paper appearing a short

while later (1927) suggests the same function. The radula may or may not possess a median, longitudinal, double row of non-articulating spines, usually recumbent, and with their apices directed toward the median line. Frequent use of the presence or absence of this character is made in taxonomic keys. The setae of the radula are articulate and may or may not be hooked at their tips. This group of setae is frequently figured by workers with white grubs. It has had no name and as far as was previously known no function had been suggested for it. In a study of the digging habits of white grubs in observation cages the writer has frequently noticed the grubs making use of this structure to rake off the mouthparts, which often become covered with soil as the larvae burrow through the soil, especially if it is very wet and sticky. Since the general term "ventral aspect of the last abdominal segment" is cumbersome, it is preferable to speak of it as the rake, or radula. The radula does not differ strikingly in the second or third instars, but in the first instar it is not well developed and some of the spines and setae are wanting.

THORACIC LEGS

The legs (Fig. 101, 102, 135, 136, 137) are normally three pairs, but *Passalus* (Fig. 3, 137) has only two well-developed pairs, with the posterior or metathoracic pair greatly reduced and specialized to function as an organ of stridulation. The nature of this organ and of somewhat similar modifications, but without reduction in size of the metathoracic leg, as occurring in the *Lucanidae*, the *Trogidae*, and some *Scarabaeidae* will be described later when the stridulating organs are discussed.

Following the interpretation of the parts of the leg (Fig. 101, 102) as given by Böving (1921) in his description of the Japanese beetle, we find a long, cylindrical coxa (*cx*) followed by a short trochanter (*tr*). The femur (*fm*) is long and slightly clavate, while the next segment (*tb*) is interpreted as the tibia with the tarsus either absent or, what is more probable, fused with the tibia, since this structure bears the single tarsal claw (*cl*). Arrow (1910, p. 11) considers the claw-bearing segment as the "tibio-tarsus," assuming that the two parts are fused into the one part. It is difficult to say what part is homologous to the small, stridulating leg of the metathorax in the *Passalidae*. In the *Coprinae* no tarsal claw is present.

In most cases, the anterior pair of legs are the shortest, the intermediate pair next in length, and the last pair the longest. The legs are not used to a great degree in walking but are important aids in digging through the soil. As pointed out previously, the *Cetoniinae* do not use their legs in walking but thrust them in the air and crawl on their backs.

SPIRACLES

The spiracles (Fig. 122, 123), although not closely studied, are probably characters of importance for the larger groups. Böving (1921) has described them in some detail for *Popilla japonica* and some allied forms, and Boas (1893) has written concerning the histological features of European Melolonthinae. Schiödt (1874) has also figured the minute structure for some European species. Each spiracle is usually surrounded by a well-defined peritreme (*p*). The peritreme in *Trox* (Fig. 123) is not so well defined and does not resemble that of other species. Normally the peritreme is a half-moon or nearly circular in form. It encloses an area known as the bulla (*b*). The peritreme is usually provided with minute openings or pores. (See the drawings of the two authors cited above.)

The thorax has but one pair of spiracles, located on the caudal margin of the prothorax. There are eight pairs of abdominal spiracles, making nine pairs in all. The meso- and metathorax and the last two abdominal segments are without spiracular openings.

The arrangement of the opening, or emargination, of the peritreme differs considerably in the various groups. In *Passalus* (Fig. 3) the prothoracic spiracle has the open, or emarginate, side of the peritreme on its cephalic margin; while in the succeeding eight segments the emargination is on the caudal margin. In most of the Scarabaeidae (Fig. 8 to 12) the condition found in *Passalus* is reversed; *i.e.*, the emargination of the prothoracic spiracle is on the caudal margin and the remaining spiracles have the peritreme "open" on the anterior margin. In *Pinotus* (Fig. 1) and other Coprinae the emargination of the peritreme of all spiracles is on the ventral margin. In *Trox* (Fig. 123) the shape of the area surrounding the bulla is markedly different from other species. It consists of an indefinite area dorso-ventrally striated and having no definite emargination of the peritreme.

ANAL ORIFICE

The anal opening, frequently called the *anal slit*, is usually figured in published illustrations of the radula. It differs considerably in form in the various groups, and some use of this is made, especially with the Lucanidae, in the appended taxonomic keys. Davis (1916, p. 266), in listing the various characters of scarabaeid larvae, refers to the anal slit as "obtuse" or "transverse." In the obtuse slit a broad angle is formed, with its vertex directed ventrally (Fig. 156 to 189), while the transverse slit is nearly straight or slightly rounded (Fig. 143 to 150). In the Trogidae (Fig. 151) it is Y-shaped, with three slits converging at a central point. This type represents an intermediate condition between that found in the Scarabaeidae and in the Lucanidae. In *Sinodendron* (Fig. 153) and *Dorcus* (Fig. 154), as well as others of the family Lucanidae, the anal slit is made up of three

slits, as in *Trox*. In *Dorcus* and others the slits are surrounded by three more or less conspicuous lobes, which are not so evident in *Sinodendron* and *Trox*. In *Passalus* (Fig. 152) the slit consists of a long transverse opening in the middle of which is a short, ventrally directed slit.

Davis (1916) has pointed out that *Phyllophaga* and *Polyphylla* (Fig. 141) larvae have an obtuse anal slit. The same condition is found in *Serica* (Fig. 140) and *Macroductylus* (Fig. 142) and probably holds good for most of the subfamily Melolonthinae. Davis writes: "The grubs of *Anomala*, *Listochelus*, and *Phytalis* are very close to those of *Lachnosterna* [*Phyllophaga*], and we are unable to satisfactorily distinguish between grubs of these four genera." In the case of *Anomala*, they may be separated from *Phyllophaga* by the presence of a transverse instead of an obtuse anal slit. Apparently most of the larvae of the Scarabaeidae have a transverse slit, for such is the condition of the specimens examined in the subfamilies Rutelinae (Fig. 144), Dynastinae (Fig. 145), Cetoniinae (Fig. 148 to 150), Aphodinae (Fig. 138), and Glaphyrinae (Fig. 139).

It is of interest to note that Riley (1870, p. 295) in a description of the larva of *Pelidnota punctata* has figured the anal slit of some lucanid which occurs in decaying wood as does also the larva of *Pelidnota punctata*. He apparently found a newly transformed adult of *Pelidnota* which he associated with the larva of the lucanid that is figured in his article.

ORGANS OF STRIDULATION

The organs of stridulation in lamellicorn larvae are of two types: those of the mouthparts, which are developed on the mandibles and maxillae; and those of the legs, in which the middle and hind legs are modified for stridulation. The stridulating organs of the mouthparts are confined to the Scarabaeidae and differ somewhat in some of the subfamilies. The Lucanidae, Trogidae, and Passallidae have no stridulating organs on the mouthparts but have the legs modified to produce sound. Schiödte (1874) was the first to describe these organs, although DeHaan (1836) had previously figured the striae on the mandibles. Schiödte's description of these structures in the Scarabaeidae is as follows:

"Chez les larves des Dynastides, des Cétonides, des Rutélides, des Mélonlonthides, des Séricides et des Coprides, il se trouve, sur la face supérieure de la tige maxillaire (*stipes maxillarium*), une crête longitudinale munie d'une rangée de dents disposées de manière à pouvoir atteindre et râcler, par le mouvement d'avant en arrière des maxilles, des granulations spéciales diversement placées et groupées sur la face inférieure des mandibules.

"Les granulations des mandibules chez les larves des Dynastides et des Cétonides (*Xylotrypes*, *Oryctes*, *Parastasia*, *Cetonia*, *Osmoderma*) sont rangées en côtes transverses assez fortes et formant une plaque à peu près elliptique, nettement circonscrite, située vers la base des mandibules, en dehors de la partie molaire. Les larves des Rutélides (*Anomala*, *Phyllopertha*) diffèrent seulement par leurs côtes beaucoup plus fines, plus nombreuses et plus serrées. Chez les Mélonlonthides (*Melolontha*, *Rhizotrogus*), des Séricides (*Serica*) et des Coprides (*Ateuchus*, *Aphodius*, *Ammonoecius*), les granulations des mandibules ne sont pas rangées en

côtes. Chez les larves des deux dernières tribus, elles sont d'une petitesse extrême et placées près de la base des mandibules; chez les larves des Mélolonthides, elles sont plus visibles et occupent un espace transversal au milieu des mandibules."

His article continues with a description of the stridulating apparatus on the legs of Passallidae, Lucanidae, and the genus *Geotrupes* of the Scarabaeidae.

The mouthpart stridulating apparatus, found only in the Scarabaeidae, consists of two types, one being more highly developed than the other. In the larvae of all Rutelinae, Dynastinae, and Cetoniinae examined, there appears on the caudal aspect of each mandible a minute series of sharp ridges, transversely arranged (Fig. 81, 82, 83, 87, 88). The longest ridges are the median ones. The others become gradually shorter to give the whole a uniform oval appearance. Opposite to these ridges of the mandibles, on the cephalic aspect of the stipes of the maxillae, is a row of teeth, which, in some cases, are decidedly blunt (Figs. 118 and 124), in others, long and pointed (Fig. 111), and in still others, long, pointed, and decidedly curved (Fig. 113) toward the distal extremity of the maxilla. They differ in number in different genera. They have not been given careful consideration in this study, but it was noted in *Anomala kansana* that one maxilla bore six curved teeth (Fig. 113) while the opposing maxilla had but one (Fig. 112). One maxilla of *Phyllophaga crassissima* (Fig. 118) had fourteen short, truncate teeth; *Ligyris gibbosus* (Fig. 124) had thirteen; *Cotalpa lanigera* (Fig. 114) five; *Euphoria inda* (Fig. 125) six; and *Amphicomma* sp. (Fig. 111) ten. These teeth, by movements of the mouthparts, rasp against the ridges on the mandibles to produce a "faint high-pitched note" (Arrow, 1910, p. 11).

In the subfamilies Coprinae and Melolonthinae the ridges of the mandibles are lacking, and in their places is a minutely rugose surface which is indefinite and difficult to discern (Fig. 84, 85). According to Arrow (1910, p. 12), this apparatus is comparatively imperfect and it "has not yet been definitely ascertained what sound, if any, is produced by these." The writer has never heard *Phyllophaga* grubs produce any sound.

In the genus *Geotrupes* of the Scarabaeidae, Schiödte and Arrow have both described the leg type of sound production, which is similar to that in the Lucanidae. Arrow points out that the hind leg is considerably shortened and "the joints appear solidified, while from the base to the tip runs a row of sharp horny teeth." These rasp against a horny area at the base of the second pair of legs, which is provided with a series of fine ridges. The rasping structures in this genus, being on the middle leg, are reversed from similar organs in the Lucanidae in which the file, or series of ridges, is on the hind leg. The writer has not seen specimens of *Geotrupes* larvae.

In the Lucanidae (Fig. 135, 136) there is a strongly chitinized area on

the coxae of the middle pair of legs which is covered with small sharp spines or tubercles. On the trochanter of the hind legs is an elongated file composed of a series of transverse ridges. The trochanter of the posterior legs is drawn across the coxae of the middle legs to produce sound. The stridulating organ of *Passalus cornutus* (Fig. 137) is frequently figured in discussions of sound organs because of the unique reduction in the size of the hind pair of legs, the parts of which are reduced to small paw-like structures that are provided with a series of small hooks which are drawn across a microscopically ridged chitinous plate on the coxae of the middle pair of legs. Gravely (1916, p. 139), in a discussion of oriental Passalidae, states that the larvae are all much alike. He figures an oriental species much like our *Passalus cornutus* of North America, which has this modification of the larval leg for stridulation.

Gravely (1915, p. 498) has described the action of the stridulating organs of the mouthparts of *Oryctes rhinoceros* as follows:

"Concerning the action of the stridulating organs of *Oryctes rhinoceros* nothing yet seems to have been published. I have had great difficulty in obtaining any evidence as to the use of the so-called stridulating organ found in the larva. When a specimen is tightly held by the head, however, it may be seen to move the mandibles and maxillae in a manner likely to bring the organ into action, and a faint rasping sound may sometimes be heard if the specimen be brought close to the ear. No definite vibrations have been felt, and the movements of the mandibles and maxillae are those which would probably be used, in order to free itself, by any insect similarly placed. Pressure on the body does not seem to induce any such movements but they are sometimes indulged in by larvae which find themselves on their back on a hard surface in the open. The movements are often greater in extent than their use for stridulating purposes requires; the mandibular part of the organ is, indeed, sometimes fully exposed at intervals, and could not then be scraped at all by the maxillary portion. The rasping seems, nevertheless, to be produced only when these movements occur. It is therefore probable that it is produced by the organs in question, and it is noteworthy that the movement of the mandibles and maxillae is often very small—as it should be to keep the two parts of the organ in contact—and that this does not interfere with the sound produced."

In conclusion of this consideration of these stridulating organs, it must be pointed out that Sharp (1918, p. 198) maintains that these mouthpart structures are "but little adapted for the purpose of producing sound."

POSTEMBRYONIC DEVELOPMENT AND BIOLOGY OF THE SCARABAEIDAE

Since the writer has had no experience with life-history studies of the Lamellicornia other than in the family Scarabaeidae, most of the following statements will be confined to that family. However, it is of interest to recall that the eggs of the Trogidae are laid in carrion while those of the Lucanidae and Passalidae are laid in partly decayed wood. Arrow (1910, p. 20) suggested the possibility of Passalidae being viviparous, but Gravely (1915, p. 495) states that, on a visit to Berlin, he called the suggestion of Arrow to the attention of Dr. Ohaus, who immediately refuted it by producing eggs of American species of Passalidae from his collections.

Eggs

Oviposition Preferences

Among the Scarabaeidae the egg-laying habits are rather diverse, even within the various subfamilies. The eggs of *Canthon laevis* are laid in a ball of dung buried in the soil. *Pinotus carolina* and *Strategus mormon* fill their burrows with manure and afterwards lay their eggs in it. According to Arrow (1910, p. 19), Lefroy has recorded the finding of an egg ball of *Heliocopris dominus* eight feet below the surface of the ground. The progeny of these dung-feeding beetles is not large, some species having been noted to lay less than a dozen eggs; others are more prolific, as Davis (1916, p. 263) has noted that individual females of *Phyllophaga* have been observed to lay between 50 and 100 eggs. In the writer's experience, fewer than 50 eggs was the rule with this genus, but this may be due, in part, to the type of oviposition cages used. The eggs of *Phyllophaga* and other Melolonthinae are laid in the ground, usually in hard, packed soil covered with vegetation, but collection studies show that they are by no means confined to this sort of soil for oviposition, as grubs are frequently found in soil that has been plowed year after year.

Among some Rutelinae (e.g., *Cotalpa lanigera*) and some Cetoniinae (*Osmoderma* spp.) there is an apparent selection of situations for oviposition near decaying wood in which the larvae must develop. The writer has found hundreds of eggs of *Pelidnota* under decaying logs and has succeeded in getting *Osmoderma* to oviposit in soil in cages on which decaying wood had been placed. Other Rutelinae lay their eggs in soil, as do the Melolonthinae, while many Cetoniinae prefer to oviposit in manure and other decaying organic matter. Eggs of the Dynastinae are deposited in decaying organic matter or in the soil about the roots of plants. One species, *Ligyrodes relictus*, lays its eggs in decaying hay and straw stacks, as

well as in manure piles; while a related species, *Ligyryus gibbosus*, lays its eggs preferably at the roots of sunflowers. The Aphodinae deposit their eggs in dung, and many species seek out and prefer the excrement of a definite animal.

Description and Length of Egg Stage

The eggs of the Scarabaeidae, being deposited by individuals of many sizes, naturally exhibit enough difference in size to make a general statement of little use. It is obvious that the eggs of smaller beetles, such as *Serica*, some *Diplotaxis*, and many others, would be considerably smaller than the eggs of larger species, such as *Dynastes* or *Strategus*. A broad statement might be made, that they vary in size from one to four millimeters. When freshly deposited they are, as a rule, elongate-oval in shape, being two or three times longer than wide. As development proceeds, there is an increase in width, so that the eggs just before hatching are much more broadly oval or nearly round. The color is somewhat variable, even within the species. Some are milky-white, others are pearly-gray. The chorion is transparent, so that previous to hatching the dark mandibles and the segmentation of the body can be discerned through it. With those species which oviposit in the soil, there is usually found adhering to the eggs a sticky secretion from the colleterial glands which causes the surrounding soil to become attached to the eggs and form an enveloping ball of earth around each egg. This ball is usually broken when searching for eggs in the soil, but parts of it can usually be seen still clinging to the egg.

Egg laying occurs in the spring and summer months. It may extend over a considerable period in some species. As far as known, none are ever carried over the winter. Table I, compiled mostly from the writer's observations under conditions as described on page 14, and with the addition of excerpts from other works, shows the length of the egg stage of the Scarabaeidae. It is interesting to note that all of the species listed belong in the four subfamilies of the Pleurosticti, very little being known of the life histories in the Laparosticti.

Egg Burster and Hatching

Many insects possess, in the late embryonic stage, certain spines which aid in the rupture of the chorion during hatching. These have been called hatching spines, ruptor ovi, or egg bursters. In the Colorado potato beetle they consist of three pairs of spines on the thorax, while in other insects the structure may be a single spine on the head. Ritterschaus (1925 and 1927) has mentioned the occurrence of egg bursters in two species of European Scarabaeidae (*Anomala aenea* and *Phyllopertha horticola*). The structure is described as two triangular-shaped, chitinized spines; one on each dorso-lateral aspect of the metathorax. Accompanying the

TABLE I.—THE LENGTH OF THE EGG STAGE IN SCARABAEIDAE

Species	Number of Eggs Hatching	Number of Days			Comment	
		Maximum	Minimum	Average		
Melolonthinae						
Strigoderma arboricola...	14	14	10	12.2	Eggs collected in field shortly after deposition.	
Phyllophaga						
Affabilis.....	54	16	10	14.3		
Bipartita.....	262	24	11	16.6		
Corrosa.....	806	28	11	18.1		
Submucida.....	84	20	13	14.0		
Vehemens.....	42	28	11	19.8		
Tristis.....	396	23	10	17.2		
Fusca.....	48	28	16	19.5		
Crenulata.....	24	20	14	18.2		
Longitarsa.....	447	19	7	12.7		
Prætermisssa.....	185	23	12	17.6		
Ephillida.....	3	15	12	13.0		
Rugosa.....	127	29	14	19.5		
Rubiginosa.....	180	24	11	17.0		
Lanceolata.....	1808	29	10	15.8		
Futilis.....	1017	38	11	21.1		
Crassissima.....	1000	27	8	16.1		
Hirticula var. comosa...	293	30	11	17.9		
Implicata.....	190	31	10	18.2		
Rutelinae—Tribe Anomalini						
Popillia japonica.....	—	27	9	14	Data from Smith and Hadley.	
Anomala binotata.....	—	11+	7+	—		
Anomala kansana.....	632	19	9	12.2		
Anomala innuba.....	119	19	11	14.6		
Rutelinae—Tribe Rutelini						
Pelidnota punctata.....	979	26	8	14.9		
Cotalpa lanigera.....	177	27	18	20.9		
Dynastinae						
Ligyris gibbosus.....	555	22	7	10.9		
Ligyroides relictus.....	4	11	8	9.3		
Ochrosidia immaculata	107	25	9	15.5		
Strategus titanus.....	—	21	15	17	Data from Smyth.	
Strategus quadrifoveatus	—	—	—	20	" " "	
Dyscinetus trachypygus	—	18	10	12	" " "	
Dyscinetus barbatus.....	—	—	—	13	" " "	
Euetheola rugiceps.....	—	—	—	14	Data from Phillips and Fox.	
Cetoniinae						
Euphoria inda.....	—	11	7	—		
Euphoria fulgida.....	140	13	8	10.7		
Euphoria sepulchralis...	27	13	9	11.8		
Cotinus nitida.....	8	19	9	13.7	Data from Chittenden and Fink.	
Osmoderma eremicola...	—	16	7	16	Data from Sweetman and Hatch.	

spine is a stiff bristle, or seta, about twice as long as the hatching spine. Since these are discernible through the chorion before hatching and are not present after the first molt, this author maintains that, by the aid of muscular contractions, they assist the embryo to break the shell during the hatching process.

Such a structure has never been described in North American Scarabaeidae. I have examined many eggs and newly hatched larvae of various species dealt with in this study and have never been able to satisfy myself of the presence of any such a specialized structure. It is true that many strong setae are present, but no strong spine such as described for these European species can be distinguished. Since Ritterschaus has figured these through the chorion of the egg and in larvae which have hatched, it seems probable that further study will show their presence in at least some North American species. It is quite probable that the many strong setae located on the back of most of the body segments aid the insect, in some degree, in its struggle to burst the egg shell.

A scarabaeid egg which is about to hatch can be readily distinguished by its more oval shape in contrast to the elongate-oval form which it presents at the time of oviposition. Moreover, before hatching, the embryo can be seen clearly through the chorion. On the ventral aspect the darkened mandibles are the most distinct, but the tips of the maxillae and antennae can be noted. On the lateral aspect the legs and the darkened spiracles are quite evident, while on the dorsal aspect the body segments and spines can be observed. The mandibles are frequently seen to open and close under the chorion, and perhaps they aid other body contractions in the rupture of the egg shell.

The breaking of the shell occurs across the back in the region of the thorax and first abdominal segments. Ritterschaus (*loc. cit.*) has figured this split as coming directly across the metathorax in the region of the egg burster. The break continues until the dorsum of the thorax is exposed, after which the head is freed and the shell is worked backwards over the end of the abdomen. In rearing cages, many of these newly hatched grubs are unable to remove this shell from the dorsal segments of the abdomen and can be observed carrying it about with them. Sometimes a portion of the shell is cast off over the head. In many instances, newly hatched grubs die before they can entirely free themselves of the egg shell. In a few cases these newly hatched larvae were seen to be feeding on the shell.

LARVAL DEVELOPMENT

Molting

Ecdysis occurs twice before the pupal molt. In two-year grubs as observed, the two molts previous to pupation occur, as a rule, during the same season that the egg is hatched, but rarely the second molt may be

delayed until the following summer. Among the three-year grubs, only the first molt occurs during the season the egg is hatched, and the second occurs the following year. To illustrate: two-year grubs hatching in 1928 would molt twice in 1928 as a general rule, but in a few instances the second molt would be delayed until 1929. The three-year species hatching in 1928 would molt once during the summer of 1928 and once in 1929. All of the grubs molt again at pupation, and generally the pupa lies within the exuvia.

In species having a one-year cycle the customary two molts occur during the growing season of summer and autumn. Occasionally, in *Cotalpa lanigera*, the grubs may undergo three molts before becoming prepupae. The time from hatching to first molt in *Cotalpa* averaged 23.6 days for 49 individuals, and 282.8 days from the first to the second molt, with extremes of 28 and 326 days; that is, some individuals molted the second time during the season in which they hatched and others delayed the second molt until the following season. The period from the second to the third molt varied from 41 to 292 days, with an average of 143.8 days. In no instance was the third molt observed to occur the first season after hatching, but a sum of the three minimum periods shows that it may be possible for the grubs to have their third molt 89 days after hatching. The low minimum of 41 days between the second and third molts was noted in cases where the second molt occurred the second season, and the maximum of 292 days is secured in those instances where the second molt occurred the first season and the third molt the second season.

The period between the second molt and the time of becoming prepupa, therefore, depends upon whether or not there is a third molt. In 19 instances where the third molt was absent, the length of the instar varied from 66 to 432 days, with an average of 334.6 days. In only one case was the time between the third molt and prepupation noted. This individual had molted twice the first season, and the third molt occurred the second summer. There were 379 days between the third molt and prepupa (fourth instar). In all cases (five) where a third molt occurred, the grubs were destined to be three-year grubs. The active larval period varied from 362 to 743 days in 21 cases noted.

The length of each instar, or the period between molts, in the genus *Phyllophaga*, has been taken as the normal period between molts in those individuals having but two molts before pupation. These data are summarized for a few of the representative species in the tables which follow. In Table II is given the average length of time between hatching and the first molt for the species listed. In addition, the maximum and minimum numbers of days between these phenomena are noted, as well as the numbers of individuals under observation. In no case was the minimum period under 11 days (*P. bipartita*), and the longest period occurred in the same species, where 63 days were required before the first molt. The average period ranges from 28 days (*P. affabilis*) to 45 days (*P. vehemens*).

TABLE II—INTERVAL BETWEEN HATCHING AND FIRST MOLT
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	16	49	19	35.8
<i>P. bipartita</i>	100	63	11	39.9
<i>P. vehemens</i>	2	47	43	45
<i>P. corrosa</i>	237	58	17	39.4
<i>P. hirticula</i>				
var. <i>comosa</i>	41	46	26	35.5
<i>P. crenulata</i>	7	54	35	44
<i>P. affabilis</i>	33	44	23	28
<i>P. tristis</i>	22	52	22	33.9
<i>P. longitarsa</i>	67	42	17	24.1

The length of the second instar is more variable, as is to be noted in Table III, which includes species with a one, two, or three-year life cycle. In general it may be said that the one-year and two-year species listed correspond more closely, in the length of the second instar, to the periods given in the minimum column, while the three-year species and some two-year species more nearly approximate the maximum dates. The shortest period noted for this instar was 7 days (*P. corrosa*) and the longest was 374 days (*P. praetermissa*). This means that the second molt may occur as early as 7 days after the first or as late as 374 days.

TABLE III—INTERVAL BETWEEN FIRST AND SECOND MOLTS
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	16	374	20	263
<i>P. bipartita</i>	34	335	284	39.9
<i>P. vehemens</i>	2	314	28	171
<i>P. corrosa</i>	136	326	7	218.1
<i>P. hirticula</i>				
var. <i>comosa</i>	41	323	266	294
<i>P. crenulata</i>	1	284	284	284
<i>P. affabilis</i>	19	304	33	198.8
<i>P. tristis</i>	22	28	10	18
<i>P. longitarsa</i>	67	286	11	69.7

To understand the length of the third instar it is necessary, because of the way in which the data were recorded, to present the figures in two tabulations (Tables IV and V). A short time before pupation the larvae cease feeding, shed their meconium, and tend to shrivel up in preparation for the change to the pupal stage. This is the beginning of the prepupal stage. The data on the length of the third instar (up to the prepupal stage) are given in Table IV, and the data on the length of the prepupal stage, which must be added to the figures in Table IV are given in Table V. It will be observed that the third instar is much longer than the others and, as mentioned previously, depends on whether the second molt occurs during the summer in which the larva hatches from the egg or whether the molt is delayed until the following summer.

TABLE IV—INTERVAL BETWEEN SECOND MOLT AND PREPUPA
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	5	429	320	397.6
<i>P. bipartita</i>	9	423	70	337.2
<i>P. vehemens</i>	2	339	66	202.5
<i>P. corrosa</i>	32	440	97	346.1
<i>P. hirticula</i>				
var. <i>comosa</i>	1	412	412	412
<i>P. crenulata</i>	1	59	59	59
<i>P. affabilis</i>	5	292	35	228
<i>P. tristis</i>	4	372	361	364.7
<i>P. longitarsa</i>	67	388	35	270.6

TABLE V—LENGTH OF PREPUPAL STAGE IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	15	12	3	6.7
<i>P. bipartita</i>	9	17	3	9.2
<i>P. vehemens</i>	3	7	7	7
<i>P. corrosa</i>	25	15	2	6.6
<i>P. hirticula</i>				
var. <i>comosa</i>	25	16	4	8.7
<i>P. crenulata</i>	2	8	7	7.5
<i>P. affabilis</i>	5	5	4	4.2
<i>P. tristis</i>	3	7	5	6
<i>P. longitarsa</i>	58	16	2	4.1

Postembryonic Changes

During larval development there are no conspicuous postembryonic changes. The most marked is the gradual increase in size. This, of course, varies considerably with the different species. Grandi (1925), in a comparison of the newly hatched larva and the larva one-year old, says that there is little difference between them except for dimensions, and goes on further to point out the slight differences which occur in those characters which present variation of any importance. These characters are the antennae, the labrum, maxillae, labial palpi, and abdomen. Of these, he notes that the antennae become longer and more slender; the labrum presents slight changes in shape; in the maxillae the change comes in the proportions of the palpi, and the same is true of the labial palpi and legs. In the abdomen the changes are more marked in the setation of the last abdominal segments. For this reason, the characters in the larval key, as herein presented, are based on third instar larvae, since no satisfactory study has yet been made of the first and second instars.

In addition to the changes pointed out by Grandi, there is a marked change in many species in the proportions of the head and body. In the first instar (Fig. 193) the head is much larger in proportion to the rest of the body than it is in the second (Fig. 194) or third (Fig. 1 to 12). Although no definite measurements have been made, it is quite evident, to one handling and feeding larvae during the summer months, that between the molts there is a slight increase in the size of the head capsule as well as a corresponding increase in the size of the thorax and abdomen. Most of this increase occurs shortly after the completion of ecdysis.

Food Habits

During the course of a series of biological studies of the family Scarabaeidae carried on at the Kansas State Agricultural Experiment Station, considerable data were amassed on the relative numbers, as well as the habitat and food preferences, of larvae of various common species. The results have been published by Hayes and McColloch (1928). Some of the data on the food preferences are taken from that publication and presented here for the sake of completeness.

Collections of larvae of this family of beetles were begun in 1916 and extended over a period of eight years, including 1923. The specimens collected were transported to the laboratory and reared to the adult stage in individual salve boxes in an underground cave. Because of the difficulty in rearing, and in some cases because of the long life-cycle, less than one-third of the numbers collected in the field were reared to adulthood for determination of the species. During the eight years 18,781 grubs were collected, of which 5,884 were matured under artificial conditions. These 5,884 reared specimens represented 17 genera, with a total of

TABLE VI—HABITAT PREFERENCE OF ALL SPECIES

Habitat	1916		1917		1918		1919		1920		1921		1922		1923		Total	
	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared	Col.	Reared
Wheat.....	123	36	17	11	24	18	202	76	1728	746	459	110	2030	860	3329	657	7912	2514
Blue Grass Lawns..	85	15	—	—	152	32	8	4	1404	199	9	1	87	25	4	3	1749	279
Oats.....	312	144	—	—	2	2	—	—	239	144	610	93	193	106	194	37	1550	526
Corn.....	44	26	103	41	215	118	264	135	274	195	48	10	281	139	165	80	1394	744
Logs and Stumps...	—	—	2	2	221	75	3	3	6	3	43	9	40	15	886	107	1201	214
Pasture.....	40	8	49	13	141	21	24	15	3	3	65	26	13	7	195	62	530	155
Manure.....	78	37	9	2	18	12	89	23	—	—	388	97	194	76	170	63	946	310
Orchard.....	4	1	1	1	—	—	1	1	—	—	37	4	93	10	56	37	192	54
Alfalfa.....	—	—	—	—	—	—	8	3	85	21	805	150	61	21	62	22	1021	217
Potatoes.....	—	—	—	—	9	6	1	1	53	15	315	35	—	—	—	—	378	57
Garden.....	5	2	—	—	31	17	103	61	45	26	93	22	115	46	146	64	538	238
Miscellaneous.....	25	1	70	29	1	1	87	50	167	79	172	73	510	203	338	140	1370	576
Total.....	716	270	251	99	814	302	790	372	4004	1431	3044	630	3617	1508	5545	1272	18781	5884

37 species. The largest number of species belonging to a single genus was the 17 species of *Phyllophaga*. The other genera distributed among the various subfamilies of Scarabaeidae contained but one, two, three, or four species.

In Table VI are shown the habitat preferences of all species collected. These are indicative of the food preferences as a whole but not as related to the individual species, which are shown in Tables VII and VIII. In Table VII it is shown that the most individuals of *Phyllophaga* were taken in blue grass sod, 234 specimens being found there. The next in preference is corn land, with 140 individuals, which is closely approached by the 126

TABLE VII.—FOOD PREFERENCE OF PHYLLOPHAGA GRUBS

Species	Wheat	Blue Grass and Lawns	Oats	Corn	Logs and Stumps	Pasture	Manure	Orchard	Alfalfa	Potatoes	Garden	Miscellaneous	Total
<i>P. crassissima</i>	23	202	7	45	—	9	2	2	19	5	45	37	396
<i>P. rubiginosa</i>	10	16	1	18	2	16	1	1	16	20	14	20	135
<i>P. rugosa</i>	18	4	6	19	—	3	—	—	6	19	36	14	125
<i>P. lanceolata</i>	45	1	—	5	—	26	1	—	—	—	—	1	79
<i>P. submucida</i>	7	—	2	6	1	3	56	—	—	—	1	3	79
<i>P. implicata</i>	10	1	3	44	1	—	1	1	—	2	4	9	76
<i>P. hirticula</i>	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>var. comosa</i>	5	—	9	2	—	1	—	—	6	—	—	1	24
<i>P. praetermissa</i>	2	8	—	—	—	3	—	—	—	—	—	—	13
<i>P. longitarsa</i>	3	—	—	—	5	—	—	—	—	—	—	—	8
<i>P. bipartita</i>	1	—	—	—	1	4	—	—	—	—	—	—	6
<i>P. futilis</i>	—	2	—	—	1	—	—	—	1	—	—	1	5
<i>P. corrosa</i>	1	—	—	—	—	4	—	—	—	—	—	—	5
<i>P. glabricula</i>	—	—	—	—	—	4	—	—	—	—	—	1	5
<i>P. fusca</i>	1	—	1	—	—	—	—	—	1	—	—	—	3
<i>P. crenulata</i>	—	—	—	1	—	—	—	—	—	—	1	—	2
<i>P. tristis</i>	—	—	—	—	—	1	1	—	—	—	—	—	2
<i>P. affabilis</i>	—	—	—	—	—	—	—	—	1	—	—	—	1
Total.....	126	234	29	140	11	74	62	4	50	46	101	87	964

larvae taken from wheat. Pasture land, with 74 grubs, ranks fifth, and probably to this type of food should be added a majority of those listed under the heading "manure" for in many cases these were found on pasture land. It is perceivable that *P. crassissima*, *P. rubiginosa*, *P. implicata*, and *P. rugosa* are quite generally distributed, while *P. lanceolata* shows a preference for wheat first and pasture sod second. The majority of the 56

grubs of *P. submucida* taken under manure were in pasture land. This species seems to have a preference for the upland soils of the region. The data on the other species are limited, but from adult collections it is known that *P. longitarsa* and *P. praetermissa* prefer the sand-hill regions along the rivers while *P. tristis* is usually taken near the oaks growing on the uplands.

The food preferences of other larvae of the family Scarabaeidae are indicated in Table VIII. In the total numbers reared, wheat shows a predominance of individuals, with oats and corn following in the order given. Analyzing the data by species brings out some interesting points. *Ochrosidia immaculata* is taken far more abundantly in wheat than elsewhere, although

TABLE VIII.—FOOD PREFERENCE OF OTHER SCARABAEID LARVAE

Species	Wheat	Blue Grass and Lawns	Oats	Corn	Logs and Stumps	Pasture	Manure	Orchard	Alfalfa	Potatoes	Garden	Miscellaneous	Total
<i>Ochrosidia immaculata</i> ..	1787	32	143	479	49	79	10	3	141	10	138	199	3070
<i>Ligyris gibbosus</i>	125	—	189	17	—	4	11	2	19	—	1	24	392
<i>Anomala binotata</i>	122	2	164	4	—	1	—	—	—	—	—	9	302
<i>Anomala kansana</i>	235	1	2	8	2	1	—	—	1	1	2	3	256
<i>Anomala innuba</i>	5	—	70	—	—	48	—	12	—	—	—	9	144
<i>Anomala undulata</i>	—	8	—	—	—	—	—	—	—	—	—	—	8
<i>Cotalpa lanigera</i>	113	—	—	28	—	—	1	—	6	—	—	1	149
<i>Pelidnota punctata</i> ...	2	—	—	—	114	—	—	—	—	—	1	1	118
<i>Ligyroides relictus</i>	—	1	—	—	—	2	120	—	—	—	—	—	123
<i>Euphoria inda</i>	—	—	1	—	—	—	41	—	—	—	—	4	46
<i>Euphoria sepulchralis</i> ..	—	—	—	—	—	3	6	—	—	—	—	—	9
<i>Aphodius</i> sp.....	—	—	—	—	—	—	53	—	—	—	—	—	53
<i>Canthon laevis</i>	—	—	—	—	—	4	—	—	—	—	—	—	4
<i>Trox</i> sp.....	—	—	—	—	—	—	—	—	—	—	—	122	122
<i>Polymoechus brevipes</i> ..	—	—	—	—	9	—	2	—	—	—	—	1	12
<i>Cremastocheilus nitens</i> ..	—	—	—	—	21	—	—	—	—	—	—	—	21
<i>Ataen us inops</i>	—	—	—	—	—	—	4	—	—	—	—	77	81
<i>Trichiotinus piger</i>	—	—	—	—	8	—	—	—	—	—	—	—	8
<i>Stephanucha pilipennis</i> ..	—	—	—	—	—	1	—	—	—	—	—	—	1
<i>Polyphylla hammondi</i> ..	—	—	—	—	1	—	—	—	—	—	—	—	1
Total.....	2389	44	569	536	204	143	248	17	167	11	142	450	4920

it occurs rather abundantly in corn and oats. The adults apparently show a preference for land that is frequently plowed. *Ligyris gibbosus* exhibits the same preference, being found most often in oats and wheat and less often in corn land. The same can be said for *Anomala binotata*, while

A. kansana occurs more frequently in wheat. *Cotalpa lanigera* occurs in wheat and corn, usually in the sand-hill area. Davis (1918) has reported this species doing considerable damage to raspberry bushes, strawberries, corn, and grasses.

The following species live in fallen logs and stumps: *Pelidnota punctata*, *Polymoechus brevipes*, *Trichiotinus piger*, and *Polyphylla hammondi*. Table VIII shows 21 individuals of *Cremastocheilus nitens* taken from logs. These were in ant nests on the surface of the soil under a log on the sand dunes. Several species show a preference for manure and decaying vegetation, such as rotten hay or straw stacks. Among these are *Ligyrodus relictus*, *Euphoria inda*, *Euphoria sepulchralis*, *Ataenius inops*, and *Aphodius* sp. The 122 individuals of *Trox* sp. listed in the miscellaneous column were taken under a dead horse.

TABLE IX—COLLECTIONS OF PHYLLOPHAGA AS DETERMINED BY REARING

Species	Year of Collection								
	1916	1917	1918	1919	1920	1921	1922	1923	Total
<i>P. crassissima</i>	15	36	40	33	196	52	18	6	396
<i>P. rubiginosa</i>	11	7	15	22	10	41	25	4	135
<i>P. rugosa</i>	14	4	9	33	22	24	14	5	125
<i>P. lanceolata</i>	2	16	9	50	1	—	1	—	79
<i>P. submucida</i>	—	2	2	—	—	—	66	9	79
<i>P. implicita</i>	6	4	4	8	20	1	28	5	76
<i>P. hirticula</i>	—	—	—	—	—	—	—	—	—
var. <i>comosa</i>	—	2	—	—	4	18	—	—	24
<i>P. praetermissa</i>	—	—	3	—	8	—	—	2	13
<i>P. longitarsa</i>	—	1	4	—	—	—	3	—	8
<i>P. bipartita</i>	—	—	1	3	—	—	—	2	6
<i>P. futilis</i>	—	—	—	—	3	—	—	2	5
<i>P. corrosa</i>	—	—	2	—	—	1	—	2	5
<i>P. glabricula</i>	—	2	—	—	—	—	—	3	5
<i>P. fusca</i>	—	—	—	—	—	3	—	—	3
<i>P. crenulata</i>	—	—	1	—	—	—	1	—	2
<i>P. tristis</i>	1	—	—	—	—	—	—	1	2
<i>P. affabilis</i>	—	—	—	—	—	1	—	—	1
Total	49	74	90	149	264	141	156	41	964

Relative Abundance

J. W. McColloch and the writer, in an eight-year study of scarabaeid larvae, made collections of grubs in all kinds of situations and reared many to adulthood. The following discussion of the various collections, for convenience, is divided into two groups. The genus *Phyllophaga*, with 17 species represented, will be considered as one unit while the remaining

16 genera will be considered jointly. Table IX shows the various species as to the year in which they were collected and not the year of maturity. The order of arrangement is based on numbers collected and not on their relationships.

As shown in Table IX, 964 individuals representing 17 species were reared from the total of 18,781 grubs of all species collected. Since many individuals of this genus failed to live through the rearing period, a percentage of those reared based on the number collected would be unfair. However, the percentage reared based on the total species gives an inkling of the relative proportions of *Phyllophaga* to other species of the family. Of the total (5,884) beetles, only 964, or 16.3 per cent, belonged to this genus. Table IX, as indicated in the column of totals, offers further data on the relative numbers of all the various species found in the locality considered. Of the 964 individuals of all species reared, *P. crassissima* ranks first, with a total of 396 individuals, or about 41 per cent; *P. rubiginosa* ranks second, with about 14 per cent; and *P. rugosa* third, with nearly 13 per cent.

If we compare the individual total of each species with the total adults collected during the first seven years (1916–1922) of the eight during

TABLE X—RELATIVE ABUNDANCE OF PHYLLOPHAGA ADULTS
AND REARED LARVAE

Rank	Species	Total Larvae Reared	Adults Collected 1916–1922	Comparative Ranking of Adult Abundance
1.	<i>P. crassissima</i>	396	31,996	First
2.	<i>P. rubiginosa</i>	135	15,130	Third
3.	<i>P. rugosa</i>	125	4,010	Fifth
4.	<i>P. lanceolata</i>	79	15,851	Second
5.	<i>P. submucida</i>	79	57	Eighteenth
6.	<i>P. implicita</i>	76	982	Tenth
7.	<i>P. hirticula</i>			
	var. <i>comosa</i>	24	1,696	Ninth
8.	<i>P. praetermissa</i>	13	115	Sixteenth
9.	<i>P. longitarsa</i>	8	909	Eleventh
10.	<i>P. bipartita</i>	6	3,523	Seventh
11.	<i>P. futilis</i>	5	10,362	Fourth
12.	<i>P. corrosa</i>	5	3,732	Sixth
13.	<i>P. glabricula</i>	5	440	Twelfth
14.	<i>P. fusca</i>	3	135	Fourteenth
15.	<i>P. crenulata</i>	2	127	Fifteenth
16.	<i>P. tristis</i>	2	114	Seventeenth
17.	<i>P. affabilis</i>	1	44	Nineteenth
18.	<i>P. vehemens</i>	0	2,001	Eighth
19.	<i>P. congrua</i>	0	135	Thirteenth

which this study was in progress (see Table X), some interesting facts are brought out. *P. crassissima*, the most abundant species among the adults collected, is seen to be also the most numerous among those species collected as grubs. *P. lanceolata*, while second in number of adults, is fourth in the grub collections. This may be, in part, due to the slightly longer life-cycle of *P. lanceolata* (Hayes, 1919). *P. rubiginosa*, while third among the adults, was second among the grubs; and *P. rugosa* was fifth in the beetle collections and third among the larvae. On the whole, these four important species rank very close, while greater differences are disclosed among the other species. An interesting observed fact is that more individuals of *P. submucida* were collected as grubs and reared to adults than were taken in the adult collections. The two species, *P. vehemens* and *P. congrua*, which ranked eighth and thirteenth, respectively, in the adult collections, were not reared from grubs.

TABLE XI—THE RELATIVE ABUNDANCE OF SCARABAEID LARVAE
OTHER THAN PHYLLOPHAGA

Miscellaneous Species of Scarabaeid Larvae	Year of Collection								Total
	1916	1917	1918	1919	1920	1921	1922	1923	
<i>Ochrosidia immaculata</i>	32	2	155	155	723	315	973	715	3070
<i>Ligyris gibbosus</i>	5	17	2	2	227	23	116	—	392
<i>Anomala binotata</i>	145	4	—	—	37	42	47	27	302
<i>Anomala kansana</i>	—	—	3	1	154	4	57	37	256
<i>Anomala innuba</i>	1	—	9	45	21	—	15	53	144
<i>Anomala undulata</i>	—	—	—	—	—	—	7	1	8
<i>Cotalpa lanigera</i>	—	—	—	—	—	1	23	125	149
<i>Pelidnota punctata</i>	—	2	10	1	1	7	5	92	118
<i>Ligyroides relictus</i>	13	—	10	19	1	74	6	—	123
<i>Euphoria inda</i>	25	—	—	—	1	14	6	—	46
<i>Euphoria sepulchralis</i>	—	—	1	—	—	4	2	2	9
<i>Aphodius</i> sp	—	—	—	—	—	—	—	53	53
<i>Canthon laevis</i>	—	—	—	—	—	4	—	—	4
<i>Trox</i> sp.	—	—	—	—	—	—	—	122	122
<i>Polymoechus brevipes</i>	—	—	—	—	—	—	12	—	12
<i>Cremastocheilus nitens</i>	—	—	20	—	—	—	1	—	21
<i>Ataenius inops</i>	—	—	—	—	—	—	81	—	81
<i>Trichiotinus piger</i>	—	—	2	—	2	1	—	3	8
<i>Stephanucha pilipennis</i>	—	—	—	—	—	—	1	—	1
<i>Polyphylla hammondi</i>	—	—	—	—	—	—	—	1	1
Total	221	25	212	223	1167	489	1352	1231	4920

In addition to the collections of Phyllophaga, 20 species representing 16 other genera of the family Scarabaeidae are available for comparison with the genus Phyllophaga. These were, for the most part, incidental to the white grub collections, but since all that were found were collected, the data available show the years of abundance as well as the relative numbers. These data are summarized for the various species and the years in which they were collected in Table XI. It will be noted that the two most numerous species are *Ochrosidia* (*Cyclocephala*) *immaculata* (Oliv.) and *Ligyrys gibbosus* (DeG.). The number of *Ochrosidia* reared (3,070 individuals) far exceeds that of any other species and is more than three times the number of all Phyllophaga combined, whose total figure is 964. It must be borne in mind, however, that the one-year life-cycle of *Ochrosidia* compared to the two-year and three-year cycles of Phyllophaga makes rearing much easier with less mortality. Space does not permit a discussion of all the facts apparent in Table XI, but it will be noted that the collection contains representatives of the most important subfamilies of the Scarabaeidae.

Hibernation

Our knowledge of the depth to which such insects as white grubs and May beetles penetrate the soil to escape the rigors of cold weather, and to pass their period of hibernation, is limited to a small number of casual observations. Only a few general statements pertaining to the subject are to be found in the literature. While writers assert that such-and-such a species passes the winter "below the frost line" or "below the plow line," no specific attention or careful study has been given to the subject. This is due, in part at least, to the difficulty of studying the habits of insects that live within the soil. Another factor involved, and perhaps the most important, is the difficulty of making specific identification of the immature stages of the specimens found in the soil. In most instances they must be reared through their developmental periods to the adult before they can be identified. Furthermore, winter studies of insects in the soil require careful excavation, involving considerable manual labor which must be done during the coldest and most disagreeable part of the year.

Criddle (1918) records that in Canada the grubs of certain species of Phyllophaga and allied genera penetrate to a depth of 74 inches, and that the beetles may burrow as deep as 47 inches during the winter. This statement indicates at what depth grubs may be found in a more northern climate, but no data are available in regard to the actual depth of the various species in the more temperate regions of the United States. No doubt the climate has a direct bearing on the subject, and the depth of penetration will vary with the region. In fact, the present study shows that white grubs do not penetrate as deeply in Kansas as Criddle observed in Canada. A discussion of the literature of this subject has been presented by McCol-

loch and Hayes (1923), and the following is taken from a discussion by these writers in collaboration with H. R. Bryson. (1928).

The depth at which these insects pass the winter is important in connection with the recommendation of fall, winter, or early-spring plowing as methods of control. In order to make such recommendations intelligently, it is essential to have definite information relative to the depth of hibernation of the insects. It was primarily to secure data along this line that the studies reported herein were undertaken. It also seemed desirable to further check the studies of McColloch and Hayes (*loc. cit.*) in the fall and spring reversals of temperature conditions on the surface and subsurface layers of soil, and the bearing of such changes upon the activities of soil insects in general.

An attempt was made to rear to the adult stage all grubs taken in this work. A summary of these rearings is presented in Table XII, which shows the number of grubs of each species identified and the depths at which they were taken. The data on *Phyllophaga lanceolata*, which are incorporated in this table, were secured from a series of excavations in a wheat field at Goddard, Kansas, March 13, 1919.

TABLE XII—SUMMARY OF THE DEPTH OF HIBERNATION
OF WHITE GRUBS

Species	Total Collected	Depth in Inches		
		Maximum	Minimum	Weighted Average
All white grubs	1,188	40	3	13.2
<i>Ochrosidia immaculata</i>	101	30	4	13.9
<i>Phyllophaga crassissima</i>	3	17	13	15.0
<i>Phyllophaga rugosa</i>	4	26	10	18.0
<i>Phyllophaga glabricula</i>	3	19	16	17.7
<i>Phyllophaga submucida</i>	1	14	14	14.0
<i>Phyllophaga rubiginosa</i>	1	14	14	14.0
<i>Phyllophaga bipartita</i>	1	15	15	15.0
<i>Phyllophaga corrosa</i>	1	16	16	16.0
<i>Phyllophaga lanceolata</i>	66	20	3	10.3
<i>Anomala innuba</i>	99	15	4	8.9
<i>Anomala ludoviciana</i>	2	30	20	25.0
<i>Diplotaxis</i> sp.	1	15	15	15.0
<i>Bolbocerosoma bruneri</i>	5	15	10	11.6

Table XII brings out the fact that the average depth of hibernation of all species was below the plow line. In fact, grubs of only two species were found above the 6-inch level in the work at Manhattan, while a few grubs of *Phyllophaga lanceolata* were taken at three to six inches at Goddard.

While very few determinations were made of the grubs of *Phyllophaga* collected at Manhattan, it is interesting to note that all were several inches below the plow line.

Grubs of *Ochrosidia immaculata* predominated in practically all collections. Out of a total of 101 grubs of this species, only 12 were found above the plow line. The remaining 89 were found at depths ranging from 7 to 30 inches, with the majority at the 14-inch level.

Of *Anomala innuba*, which ranked second in number of grubs identified, 99 specimens were taken. This species does not burrow downward to any great extent for hibernation. The average depth for it was 8.9 inches, with extremes of 4 and 15 inches. *Anomala ludoviciana*, on the other hand, apparently burrows deeply into the soil, as evidenced by the two specimens taken at depths of 20 and 30 inches.

Pupation.—In a previous paragraph mention was made of the preparation made by the larva in anticipation of the transformation to the pupal stage. This period of inactivity, known as the prepupal stage or semipupal stage, is of short duration before the actual molt to the pupal condition occurs. The period is characterized by internal activity, a cessation of feeding, some body shrinkage, and the cleaning out of the alimentary canal. The final molt having been completed, the pupa has now assumed a condition more nearly like the adult form. When freshly transformed, the body is a creamy white, but as development proceeds many of the adult colors are assumed. Hayes and McColloch (1920) have pointed out that during the later stages of development sexual differences of the adult may be distinguished in the antennae and the genitalia, which may be discerned through the cuticula of the pupa. In many cases, these characters are apparent throughout the last half of the pupal stage.

Pupation occurs in late summer and autumn in many species (e.g., *Phyllophaga*), and transformation to the adult occurs shortly thereafter, to enable the insect to pass the winter in the adult stage. Others (e.g., *Anomala*) pupate in the late spring and early summer, and at the end of the pupal period, after a few days of inactivity, are ready for flight. In the case of those species transforming in the fall it is usually stated in the literature that the winter is passed by the adult at the place of pupation, usually within the exuvia of the pupa. In observations made by McColloch and the writer there is some reason for believing that many adults leave this place of pupation and burrow beneath the frost line.

No systematic study has been made of the pupae of the *Lamellicornia* and no keys are available for their identification. Causal observation indicates that there are many differences, and when enough material becomes available it may be possible to describe their recognition characters. It is noteworthy that most pupae of the *Melolonthinae* are characterized by a pair of pointed caudal appendages, while *Anomala* and a number of other

genera have a rounded, blunt caudal end. Without going into details of the morphology of the pupa, it is sufficient to point out that most of the external characters of the adult are apparent (Fig. 195).

The Passalidae and Lucanidae pass the pupal period in the decaying wood in which they develop. The coprophagous Scarabaeidae, as a rule, pupate and remain within the ball or mass of manure in which the larvae have developed, while higher Scarabaeidae may merely lie within the molted larval exuviae in the soil. A number of Scarabaeidae, such as *Pelidnota punctata* and many Cetoniinae (e.g., *Euphoria*), construct a cocoon in which the pupal period is undergone. In the case of *Pelidnota*, the cocoon consists of fragments of wood, while in the Cetoniinae (e.g., *Euphoria*) it is made of bits of manure in which the larva grew. Others may use the soil or root-fibers. These cocoons, made of the food material, are oval in form. The outer surface is rough while the inner walls are smooth and polished. They are built by the larva before the transformation of the pupal stage, and the material which holds the structure together is a glandular secretion ejected from the hind intestine. The larva, by its mouthparts and body movements, is able to mold the material into a compact water-tight cocoon. The length of the pupal stage in the many species varies from a week or more to a month and even longer in cooler weather. Emergence is accomplished by a splitting of the cuticula along the back.

LENGTH OF LIFE-CYCLE

Melolonthinae

The length of the life-cycle in the subfamily Melolonthinae is extremely variable. It has long been known that *Melolontha melolontha* requires three years for development in France and southern Germany and four years in northern Germany. In Mauritius it has been found that *Phytalus smithi* Ar. has a life-cycle of slightly over one year (De Charmoy, 1912).

Although the species of Phyllophaga have been known as important pests for a number of years, only scanty information has been available concerning their life-histories, particularly with reference to the length of the various stages. This is due, in a large measure, to the fact that practically all of their period of development is spent beneath the surface of the soil, where it is difficult to observe their life activities. Chittenden (1899) was the first to report the rearing of a species of this genus. He found, in the case of one individual of *P. fervida*, that 781 days were required from the date of egg laying to the transformation of the pupa to the adult. This makes a life-cycle of three years for the species if the winter period of adult hibernation is included. Davis (1916), reporting on the length of the life-cycle of 18 species of the genus, notes in his summary that one species, *P. tristis*, invariably has a two-year period in the region of Lafayette, Indiana, and eleven other species, namely, *P. fervida*, *P. fusca*, *P. vehemens*,

P. rugosa, *P. ilicis*, *P. grandis*, *P. fraterna*, *P. hirticula*, *P. inversa*, *P. bipartita*, and *P. congrua*, without exception, have a three-year life-cycle. Two species, *P. crenulata* and *P. crassissima*, have a three-year cycle that may be extended to four years, and certain other species, as *P. futilis*, *P. ephilida*, and *P. implicata*, ordinarily have a three-year cycle that is often reduced to two years. From this it can be seen that the more important species have, in the latitude of Lafayette, a three-year cycle. Smyth (1917) has found that the life-cycle of *P. vandinei* occupied approximately one year in Porto Rico. These citations contain practically all our knowledge of the life-cycle of members of the genus, and except for the work of Smyth very little has been learned concerning the length of the immature stages.

In a study of the life-history and development of white grubs carried on by the writer in Kansas, seventeen species of the genus *Phyllophaga* were reared in varying numbers from the egg to the adult state. The development of one species, *P. lanceolata*, was described in 1919 and six others in 1920. In 1925, ten others were described and a comparison of their development made with those previously reported. To generalize, it can be asserted that the results are in accord with those of Davis in showing a decided variation of the length of the life-cycle in most of the species, this variation being found in the length of the larval period. For example, some species have, in the vicinity of Manhattan, Kansas, either a one-, two-, or three-year life-history.

With the exception of four species, *P. affabilis*, *P. submucida*, *P. longitarsa*, and *P. lanceolata*, all of the *Phyllophaga* reared by the writer pupate in the fall and pass the winter as adults. Accordingly, in considering the life-cycle, eight or nine months should be added to the figures presented in the following table to arrive at the total period of life from the time of oviposition to the normal time of death. In the four exceptions noted above, pupation occurs in the spring or early summer and the adults emerge soon after transformation.

To further compare the life-cycle of *Phyllophaga*, it should be noted that Davis (1916) found a two-year cycle in *P. tristis* and *P. lanceolata*; a two- and three-year period for *P. burmeisteri*, *P. futilis*, and *P. implicata*; a three-year period for *P. arcuata*, *P. bipartita*, *P. congrua*, *P. fraterna*, *P. fusca*, *P. grandis*, *P. hirticula*, *P. ilicis*, *P. inversa*, *P. rugosa*, and *P. vehemens*; and a three-year and possibly a four-year cycle in *P. crassissima* and *P. crenulata*.

Smyth (1917), in Porto Rico, found for 14 complete records of *P. vandinei* an average period of 306 days from egg to adult with a maximum of 395 days and a minimum of 212 days, or expressed in months, from seven to thirteen months with an average of about ten months. Except in the case of *P. tristis*, this is one of the shortest life-cycles reported. It is somewhat shorter, but is probably comparable to the one-year periods of

P. affabilis and *P. longitarsa* as here recorded. Criddle (1918) reports that *P. nitida*, *P. drakii*, *P. anxia*, and *P. rugosa* have in Manitoba, Canada, a four-year life-cycle, but gives no definite data on the length of the various stages.

Based on actual rearings by the writer, the summaries of the life-cycles of the 17 species under observation are given in Table XIII.

TABLE XIII—SUMMARY OF THE LIFE-CYCLE IN THE GENUS PHYLLOPHAGA

Species	Number of Individuals Reared	Number of Days from Egg to Adult			Life-cycle in Years
		Maximum	Minimum	Average	
<i>P. affabilis</i>	4	389	369	376.6	1
<i>P. bipartita</i>	3	815	495	703.0	2 and 3
<i>P. corrosa</i>	19	791	429	501.8	2 and 3
<i>P. submucida</i>	13	734	708	720.3	2
<i>P. vehemens</i>	3	838	459	591.3	2 and 3
<i>P. tristis</i>	4	474	137	380.0	1 and 2
<i>P. fusca</i>	1	461	461	461.0	2
<i>P. crenulata</i>	1	424	424	424.0	2
<i>P. longitarsa</i>	48	701	327	356.4	2 and 3
<i>P. praetermissa</i>	2	811	434	628.5	2 and 3
<i>P. rugosa</i>	21	836	445	735.7	2 and 3
<i>P. rubiginosa</i>	29	839	447	791.5	2 and 3
<i>P. lanceolata</i>	23	723	357	675.7	1 and 2
<i>P. futilis</i>	16	494	457	469.7	2
<i>P. crassissima</i>	81	816	449	588.3	2 and 3
<i>P. hirticula</i> var. <i>comosa</i> ...	2	789	780	784.5	3
<i>P. implicata</i>	22	790	442	470.4	2 and 3

Other members of the subfamily are little known. The rose chafer, *Macrodactylus subspinosus*, has been studied and found to have a one-year life-history. Other important genera, such as *Polyphylla*, *Serica*, *Diplo-taxis*, and *Dichelonyx*, are practically unknown as far as knowledge of their life-history is concerned.

Rutelinae

It is evident that there are two distinct types of development in the two tribes of the subfamily Rutelinae. In the tribe Anomalini there appears to be invariably a one-year life-cycle, while in the tribe Rutelini it is known that at least two years and often three years are needed to complete the life-history.

In the Anomalini, Hadley (1922) has pointed out that *Popillia japonica* requires one year to develop. The writer (1918) has shown that *Anomala binotata* matures in one season. The larvae require, on an average, 83

days to develop, and pupation occurs in the fall. On the contrary, *Anomala innuba* normally matures in the spring, but only requires one year to complete growth. Two instances were noted wherein the larvae of *A. innuba* pupated in December. *Anomala kansana* also has a life-cycle quite similar to that of *A. innuba*. It has also been shown (Hayes, 1921) that *Strigoderma arboricola* Fab., another Anomalini, has a one-year life-cycle, in which development is completed in from 351 to 358 days. In this case the larvae pass the winter and pupate in the spring. In the tribe Rutelini, *Pelidnota punctata* requires two years to mature, while *Cotalpa lanigera* needs either two or three years (Hayes, 1925). A summary of the life-cycle in this subfamily, based mostly on rearings by the writer, is given in Table XIV.

TABLE XIV—SUMMARY OF THE LIFE-CYCLE IN RUTELINAE

Species	Number of Individuals Reared	Number of Days from Egg of Adult			Life-cycle in Years
		Maximum	Minimum	Average	
Anomalini					
<i>Anomala binotata</i>	—	100	119	—	1 year
<i>Anomala innuba</i>	—	330	356	342.9	1 year
<i>Anomala kansana</i>	16	376	339	368.3	1 year
<i>Strigoderma arboricola</i>	4	351	358	—	1 year
<i>Popillia japonica</i> ^a	—	—	—	—	1 year
Rutelini					
<i>Pelidnota punctata</i>	1	698	698	698	2 and prob- ably 3 years
<i>Cotalpa lanigera</i>	21	416	806	604.6	2 and 3 years

^a Data on maximum and minimum periods not available.

Dynastinae

The subfamily Dynastinae is remarkable for the fact that it contains some of the largest coleopterous insects. One has only to recall such genera as *Dynastes* and *Strategus* to realize this fact. The group contains a number of species whose depredations on crops make them of considerable economic importance, especially in the southern part of the United States and in the West Indies. One species, *Ochrosidia* (*Cyclocephala*) *immaculata* Burm., is very injurious in the larval stage to the roots of staple crops in the central states; and another, *Ligyryus gibbosus* DeGeer, known as the carrot-beetle or muck-worm, is destructive in the adult stage to carrots, sunflowers, and other plants. Both of these have been under observation during the course of this study. *Ochrosidia immaculata* has been reported under the name of *Cyclocephala villosa* (Hayes, 1918) and the life-cycle was given as one year. Likewise, *Ligyryus gibbosus* was found (Hayes, 1917)

to have a one-year life-cycle. *Ochrosidia* differs from *Ligyris* in passing the winter as a larva and maturing in the spring.

Smyth (1916) has reported on the period of development of five species representing three genera of this subfamily. He found that *Strategus titanus* Fab., in Porto Rico, required an average of 338 days to reach maturity, *Strategus quadrioveatus* Beauv. required slightly over one year, and *Ligyris tumulosus* only 77 days. Two other species, *Dyscinetus trachypygus* and *Dyscinetus barbatus*, complete their growth in 104 and 144 days, respectively. Phillips and Fox (1917) report the development of *Euetheola rugiceps* in about 88 days. Smyth (1920) made further reports on the life-cycle in *Strategus*.

The writer has reared three species of this subfamily, *Ligyroides relictus*, *Ligyris gibbosus*, and *Ochrosidia immaculata*. A summary of the chief points of interest in their development is given here.

Adults of *L. gibbosus* are present in the soil throughout the winter and early spring. During the latter part of April or the first few days of May, and continuing throughout the summer, they emerge at night and fly to lights, returning to the soil before daybreak. During the summer of 1916, eggs were plentiful from the last of May to late in July. Larvae were present from June throughout the remainder of the summer and early fall, and pupae from the last of July to the last of October. The length of each stage of development is shown in Table XV.

Ligyroides relictus is to be regarded as a beneficial species, living as it does in manure and rotting haystacks and thus materially hastening the processes of decomposition. Smith (1902) reported the beetles injuring the roots of hardy pyrethrums and the roots of sunflowers, but his statement that the species is smaller than the ordinary June-bug and more roughly sculptured, leads to the suspicion that his determination was incorrect. These two characters and the habit of attacking sunflowers would suggest that *Ligyris gibbosus* was the species in question. Smith appears to be the only writer who considers *Ligyroides relictus* as an injurious species. There are no citations in the literature treating of the life-history of the species, and scarcely any habits are mentioned except that the beetles and grubs live in decaying vegetable matter. The average periods of development of the different stages have been found to be: for the egg stage, 9.3 days; the active larval period, 46 days; the prepupal period, 4.1 days; and the pupal period, 13.1 days. The total of 72.4 days for complete development thus approximates very closely the full period computed from the length of the different stages. Davis (1916) has reported that the species develops in one year, but gives no data on the length of stages. The beetles appear above ground in April or May for the spring flight, returning to the soil each day, where mating occurs. They disappear for a short time in June

and July, and the new brood appears in July and August for a second period of flight.

The genus *Ochrosidia* (*Cyclocephala*) contains some of our common and most injurious white grubs. Forbes (1891, p. 40) reports the grubs of *O. immaculata* infesting grass-land, corn on sod, roots of corn, and young oats. Titus (1905, p. 14) found them at the roots of grass and sugar-cane stubble, and Riley (1870, p. 307) recorded them in strawberry beds. Davis (1916, p. 264) states: "*Cyclocephala immaculata* is frequently found in compost heaps and in cultivated fields, and may obtain its full growth on decaying matter alone or may become a serious field pest, damaging crops similar to those attacked by *Lachnosterna* grubs." To summarize, the life-cycle of *O. immaculata* is one year. Adults appear at lights in June, July, and early August. Eggs, which are laid in soil, hatch after 9 to 25 days. The larva passes the winter in hibernation. The larval stage was found to average 347 days. The pupal stage varied in length from 8 to 24 days.

A comparison of the life-cycles of these three species with others reported in the literature is given in Table XV. In this table it is to be noted that, of the species whose life-history is known, the average period of development ranges from 72 days, or slightly over two months for *Ligyrodes*, to 430 days, or more than a year, for *Strategus quadrifoveatus*.

TABLE XV—SUMMARY OF THE LIFE-CYCLE IN DYNASTINAE

Species	Egg Stage			Larval Stage			Pupal Stage			Egg to Adult
	Average	Max.	Min.	Average	Max.	Min.	Average	Max.	Min.	Average
<i>Ligyrodes relictus</i>	9	11	8	50	—	—	13	26	9	72
<i>Ligyris tumulosus</i> ^a	13	—	—	55	—	—	14	—	—	77
<i>Ligyris gibbosus</i>	10	22	7	59	80	43	19	29	11	88
<i>Ochrosidia immaculata</i>	15	25	13	347	384	335	17	21	15	379
<i>Strategus titanus</i> ^a	17	21	15	344	—	—	23	24	—	338
<i>Strategus quadrifoveatus</i> ^a	20	—	—	385	—	—	27	—	—	430
<i>Dyscinetus trachypygus</i> ^a	12	18	10	81	—	—	13	16	12	104
<i>Dyscinetus barbatus</i> ^a	13	—	—	106	—	—	15	18	13	144
<i>Euethola rugiceps</i> ^b	14	—	—	60	—	—	14	—	—	88

^a Data from Smyth (1916).

^b Data from Phillips and Fox (1917).

Arrow (1910, p. 259), in his summary of the habits and metamorphoses of this subfamily, points out the following facts. They are mostly confined to the warmer climates and are of somewhat retiring habits, and our knowledge of their metamorphoses and modes of life is exceedingly scanty. With but few exceptions they are nocturnal or crepuscular and are not easily

found, and in few cases have their early stages been traced. He points out the increase in the size of the eggs, which is discussed on a previous page, as being characteristic of most scarabaeid eggs. Further comment is made that the larvae "do not differ in any marked degrees from those of the Cetoniinae and allied subfamilies," and like the Cetoniinae feed upon decaying vegetable matter, and sometimes upon living roots or woody tissues. A discussion of the nest-building habits of *Strategus antaeus*, as quoted from Manee (1908), shows these larvae to feed first on leaves stored in the nest and then probably on oak roots. Various Dynastinae are known to feed on the roots of grasses, one is known to destroy the roots of sugar cane, and *Oryctes nasicornis* is found in the refuse-heaps of tanneries, where the larvae feed on the decomposed bark.

Cetoniinae

Several members of the subfamily Cetoniinae are injurious to vegetation in the United States. Chief among these are the bumble flower-beetle, *Euphoria inda*, and the green June-beetle, or fig-eater, *Cotinus nitida*. As a rule, the mandibles of the adults of this subfamily are poorly developed and are fitted only for the eating of such light foods as pollen and sap.

There is very little American literature on the life-history of American species of this group. *Euphoria inda* is commonly assumed, and probably correctly, to have a one-year life-cycle, and the green June-beetle, *Cotinus nitida*, has been reported by Chittenden and Fink (1922) to have a one-year period of development. In the present study, a number of species have been under observation, such as *Euphoria inda*, *Trichiotinus piger*, *Osmoderma eremicola*, and *Cremastochelius nitens*. The life-cycle of none of these has been completely worked out, but two species, *Euphoria fulgida* and *Euphoria sepulchralis*, have been carried through to maturity and the results are here summarized (Hayes, 1925).

TABLE XVI—SUMMARY OF THE LIFE-CYCLE IN CETONIINAE

Species	Number of Days from Egg to Adult			Length of Life-cycle
	Maximum	Minimum	Average	
<i>Euphoria fulgida</i>	434	323	381.3	1 year
<i>Euphoria sepulchralis</i>	123	74	92.9	1 year
<i>Euphoria inda</i>	—	—	—	1 year
<i>Cotinus nitida</i> ^a	—	—	—	1 year
<i>Osmoderma eremicola</i> ^b	—	—	—	3 years

^a Data from Davis and Luginbill, 1921.

^b Data from Sweetman and Hatch, 1927.

Arrow (1910, p. 24) says of this subfamily, "Of the metamorphosis and habits of the species we know lamentably little." There are, according to him, about 2,500 species in the world. Of those occurring in America but few are of economic significance, and except for the green June-beetle, *Cotinis nitida*, three species of the genus *Euphoria*, and one of *Osmoderma*, nothing has been done toward working out their life-histories. Recently Sweetman and Hatch (1927), in rearing a larva of *Osmoderma eremicola* for 18 months, concluded that, allowing for outdoor periods of hibernation, the life-cycle would be three years for this species. It is interesting to note that all whose life-cycle has been studied require but one year to develop while *Osmoderma* with entirely different habits requires a much longer time. The little that is known of the development in this subfamily is summarized in Table XVI.

Laparosticti

For an interesting account of the biology of the Coprinae and other dung-feeding larvae, the reader is referred to Fabre's *The Sacred Beetle and Others* (English translation, 1924). Here is to be found this author's study of the development of the sacred beetle (*Scarabaeus sacer*), the *Gymnopleuri*, *Copris*, *Onthophagus*, and *Geotrupes*. Space will not be taken here to quote it. No complete American work has been done on any of our species of the subfamily. Neither has there been any investigation into the length of life of our Aphodinae. The following account of this subfamily is a translation of Schmidt's account in *Genera Insectorum*, fascicle 110, (1910).

The life-history and development of the Aphodinae are little or not well known. It is generally observed that their eggs are laid in dung, from which the developing larvae obtain their nourishment, and that pupation occurs in or under the food material. Many species apparently prefer and seek out the excrement of a definite animal. Certain species develop in the excrement of the sheep or deer, others in that from cattle, some from horses; while others may prefer either that of horses or cattle. Certain European species are known to develop in human wastes. Hubbard has reported *A. troglodytes* as living in the burrows of the land tortoise, *Gopherus polyphemus*, and Chapman states that *A. porcus* lays its eggs in the brood chambers of the scarabaeid larvae, *Geotrupes*, or the material upon which the *Geotrupes* feed. Another species occurs only in rabbit dung. *Psammobius* and *Rhyssenus* inhabit sandy regions. Their habits have not been studied, but it is thought that some species of *Rhyssenus* live on vegetable materials while others live in dung. Ohaus has noted some species of *Ataenius* in dung and others under the bark in rotten wood of fallen trees. Some exotic genera of this subfamily (*Euparia* and *Friedenreichi*) live with ants, while others (*Chaetopisthes*, *Corythoderus*, and *Termitodius*) inhabit termite dwellings.

TAXONOMY

Early students of American insects confined themselves to a study of the anatomy and classification of adult insects and the working out of their life-histories. This has resulted in descriptions of numerous new genera and species from adult characters and the description of the eggs, larval and pupal stages, and the host plants of numerous species. The number of known life-histories has been greatly increased by the establishment of state and federal experiment stations and the appointment of entomologists for the study of injurious and related species. There has been a great increase in the number of persons interested in the study of immature insects; and there have been published, not only in Europe but also in America, many systematic studies attempting to furnish tables for the identification of immature as well as adult insects. All classification is based on anatomical characters and any attempt at identification must be preceded by morphological studies. The anatomy of immature insects in many cases, while similar in general to that of the adults, is frequently very different, especially when the insects are examined in detail. The larvae contain many structures peculiar to themselves, being in most cases fitted to live a life very different from that of the adults.

A study of the anatomy of immature insects is of value from three points of view: ontogeny, morphology, and classification. It has been shown repeatedly that the complete history of the individual—its ontogeny—throws much light upon the relationship of organisms and upon their differentiation, not only as to species and genera but also as to families and orders. Investigators have found that what had been considered as a single species, from a study of the adult alone, proved to be a complex of two or more species when the immature stages were known, and that characters previously believed to be worthless could be used for separating the adults. Ontogenetic and morphological studies should proceed hand in hand. Many structures that are complex and difficult to interpret in the adult are easily understood by a comparison with the conditions found in immature insects. By comparative studies of this sort, the homology and homodynamy of various structural parts are easily determined. While it is impossible, without at least some morphological knowledge, to attempt the identification of adult specimens, such knowledge is equally pertinent for one undertaking the study of the anatomy of immature insects. The classification and identification of such insects is of the greatest value to the economic

worker, because the investigator in this field almost invariably meets with the stages that are doing the damage—the nymphs or larvae—and, unless it is a species with which he is familiar, it would be impossible to identify the pest, if no analytical tables were available, until the adult has been bred. It is hoped that by a careful study of the morphology and classification of immature insects, the labor of identification can be lessened.

With these facts in mind, the foregoing morphological studies have been made for the purpose of producing analytical keys to the various groups of white grubs. The author realizes their incompleteness. This is due, in great part, to the fact that many species are yet unknown, that in many instances only one or two specimens of known species are available and no extended consideration of the problem of variation can be made at this time because of the present state of our knowledge of the group. The following keys are therefore submitted as a preliminary step toward the further progress of the work. In the key to genera a few known species have been included. This key appeared in a recent paper by the writer (1928) and is here included with corrections and additions. It is gratifying to note, in view of the previously published statements that larvae of these families could not be separated, that one of Prof. J. W. McColloch's student's reports that this key, as it first appeared, has been helpful in his work with white grubs. The key to species of the genus *Phyllophaga* contains less than one-third of the known North American species of this genus, but until further progress is made with biological studies of the group little advance can be expected in our acquaintanceship with the many species now unknown in the larval stage.

LARVAL KEY TO FAMILIES OF THE SUPER-
FAMILY SCARABAEOIDEA

1. Posterior pair of legs small, undeveloped (Fig. 137); coxae modified into scraping, stridulating apparatus; antennae three-segmented (Fig. 94); body segments not distinctly divided into annulets and nearly devoid of spines and setae (Fig. 3). PASSALIDAE, genus *Passalus*
1. Posterior pair of legs normally developed, legs may or may not be used for stridulation (Fig. 135, 136); antennae four or five-segmented; body segments usually distinctly divided into annulets and more or less covered with spines and setae 2
2. Anal segment not trilobed on caudal aspect, legs not modified for stridulation except in *Geotrupes* (Figs. 1, 12). SCARABAEIDAE
2. Anal segment trilobed on caudal aspect (Fig. 151, 154); meso- and metathoracic legs modified for stridation (Fig. 135, 136) 3
3. Labrum usually biemarginate on its distal margin, trilobed (Fig. 33, 36); emargination of peritreme of anterior spiracles on caudal margin as is the case with the remaining spiracles; anal segment strongly trilobed; larvae feed in wood (Fig. 2). LUCANIDAE
3. Labrum not biemarginate on its distal margin, more rounded, not trilobed on distal margin (Fig. 25); spiracular peritreme of all segments small, open on dorsal margin, poorly defined (Fig. 123); anal segment feebly trilobed (Fig. 151); larvae feed in carrion (Fig. 7) TROGIDAE, genus *Trox*

LARVAL KEY TO THE SUBFAMILIES OF SCARABAEIDAE

1. Galea and lacinia of maxilla not fused (Fig. 98, 100), that is, the mala is deeply bifid; usually coprophagous larvae. LAPAROSTICTI 2
1. Galea and lacinia of maxilla fused to form the mala (Fig. 97, 104); mostly "leaf chafers" PLEUROSTICTI 6
2. Tarsi without claws (Fig. 1), a distal seta may be present; abdomen strongly "humped" on the dorsum (Fig. 1); labrum trilobed and biemarginate (Fig. 64). 3
2. Tarsi with claws or the tarsus is bilobed on its distal end, abdomen not "humped" on the dorsum. 5
3. Antenna four-segmented. COPRINAE, genus *Copris*
3. Antenna five-segmented 4
4. Tarsus strongly rounded or blunt on its distal end; tormae of labrum (Fig. 55, *l*) not meeting on the median line; ental setae of lateral lobes of the epipharynx (Fig. 55, *ll*) numerous (more than eight). COPRINAE, genus *Canthon*
4. Tarsus terminating in a long seta; tormae of labrum meeting on the median line (Fig. 67, *l*); ental setae of lateral lobes of the epipharynx scarce (usual one on each lobe) COPRINAE, *Onthophagus* (Fig. 4)
5. Tarsus without claws, bilobed on its distal end; posterior pair of legs considerably shortened (not as much so as in Passalidae); second and third pairs of legs modified for stridulation GEOTRUPINAE, genus *Geotrupes*
5. Tarsus with claws which are longer than trassus; legs not modified for stridulation; third pair of legs not noticeably shortened; body densely setaceous (Fig. 139); anal slit transverse (Fig. 139) GLAPHYRINAE, genus *Amphicoma*
6. Mandibles on their caudal aspect without an oval, stridulating area made up of transverse striae (Fig. 84); radula usually with two longitudinal rows of mesad pointing spines (not present in Serica) (Fig. 156 to 189); anal slit in the form of an obtuse angle (Fig. 156 to 189) MELOLONTHINAE
6. Mandibles on their caudal aspect, with a distinct oval, stridulating area made up of transverse striae (Fig. 81, *sa*); with or without two longitudinal rows of mesad pointing spines on radula; anal slit not angulate (Fig. 138) and more transverse. 7
7. Labrum symmetrical (*Stephanucha* is not symmetrical but it is a rare species), usually trilobed (except in *Trichiotinus* which is usually recognized by the presence of ocelli): epipharynx with a conspicuous, curved row of small spines in the region of the distal sensory area (Fig. 57, *st*); dorsum of abdomen behind the last spiracle-bearing segment not divided transversely by an impressed line thus appearing as one segment (Fig. 11); some species are "black crawlers," others found in soil, wood, and manure. CETONINAE
7. Labrum asymmetrical, not trilobed; epipharynx without a conspicuous, curved row of small spines in the region of the distal sensory area (Fig. 42); dorsum of abdomen behind the last spiracle-bearing segment divided transversely by an impressed line making it appear as two segments (Fig. 10); species of varied habits. 8
8. Ental aspect of the labrum with a series of transverse striae on the lateral margins at bases of lateral setae (Fig. 40, *st*) Tribe Anomalini RUTELINAE
8. Ental aspect of the labrum without a series of transverse striae on the lateral margins at bases of lateral setae (Fig. 50) 9
9. Stridulating teeth of maxillae (Fig. 106, *ms*) sharply pointed and curved, apices directed distally (Fig. 114); distal segment of maxillary palpus usually without a distinct, setaceous sensory area Tribe Rutelini RUTELINAE
9. Stridulating teeth of maxilla not pointed but strongly truncate being as broad as long, not curved, and not directed distally (Fig. 124); distal tooth of the series of stridulating maxillary teeth twice as wide as the others in the series; distal segment of the maxillary palpus usually ending in a setaceous sensory area. DYNASTINAE

LARVAL KEY TO GENERA OF SUBFAMILY MELOLONTHINAE

1. Anal slit obtusely angulate, not trilobed (Fig. 156); tarsal claws of posterior legs less than half as long as claws of the other legs; distal sensory area of epipharynx usually with seven to eight strong spines (Fig. 25). A few species of *Phyllophaga*, e.g., *lanceolata* (Fig. 26), have less than seven spines but can readily be distinguished by the lateral striae of the epipharynx. 2
1. Anal slit more acutely angulate, faintly trilobed (Fig. 140); tarsal claws of posterior legs more nearly equal in length to the claws of the other legs, never less than half as long; distal sensory area of epipharynx never with more than four strong spines (Fig. 31, *sp*) . . . 3
2. Longitudinal double row of spines of radula short, scarcely more than eight spines to a row (Fig. 141); head dark brown in color; dorsum of abdominal segments very densely spinose; striations of lateral margins of epipharynx indistinct (Fig. 25); epipharynx never with a submarginal, distal row of striae *Polyphylla*
2. Longitudinal double row of spines of radula longer, usually more than ten spines to a row (Fig. 156); head light yellow in color; dorsum of abdominal segments less densely spinose; striations of lateral margins of epipharynx distinct (Fig. 26, *st*), epipharynx with a submarginal, distal row of striae, sometimes difficult to observe in some species (Fig. 26, *sms*) *Phyllophaga*
3. Epipharynx with three strong spines in distal sensory area (Fig. 31); radula with a conspicuous transverse row of spines (Fig. 140) *Serica*
3. Epipharynx with four strong spines in distal sensory area (Fig. 34) 4
4. Setae of radula not hooked at the tip; presence or absence of double longitudinal rows of spines on radula questionable;¹ Distal end of abdomen sparsely clothed with shorter, stronger setae; claws of posterior tarsi less than half as long as those of other tarsi. *Diplotaxis*
4. Setae of radula hooked at the tip (Fig. 142); radula with a short, double row of longitudinal spines; distal end of abdomen densely clothed with long delicate setae; anal opening sharply acute; claws of posterior tarsi equal in length to claws of other tarsi. *Macroductylus*

LARVAL KEY TO GENERA OF SUBFAMILY RUTELINAE

1. Ental aspect of the labrum with a series of transverse striae on the lateral margins near bases of lateral setae (Fig. 41, *st*) Tribe ANOMALINI 2
1. Labrum without such transverse striae on its ental lateral margins (Fig. 44) Tribe RUTELINI 4
2. With two of the four spines of the distal sensory area of the epipharynx strongly fused at the base making a large spine with its distal end bifid (Fig. 52, *sp*); longitudinal, double row of spines of radula parallel, not divergent, with eight spines in the left row and nine in the right row *Strigoderma arboricola*
2. Without two spines of the distal sensory area of the epipharynx fused at base to form a bifid spine; longitudinal double row of spines of the radula either parallel or diverging posteriorly 3
3. Radula with longitudinal rows of spines short, about seven spines in each row; rows strongly divergent posteriorly; sensilliae of distal sensory area of epipharynx at bases of distal spines about equal in size and arranged nearly semicircularly (Fig. 41) *Popillia japonica*
3. Radula with longitudinal rows of spines usually longer, with twelve to thirteen spines in each row (Fig. 143); rows more or less parallel and frequently converging posteriorly;

¹ The only specimen of "Diplotaxis" available does not show the radula distinctly. A specimen in the Illinois Natural History Survey Collection labeled "Diplotaxis" is apparently a species of *Serica*.

- sensilliae of distal sensory area of epipharynx at bases of distal spines unequal in size and not arranged as definitely in a semicircle (Fig. 40, 43, 46)..... *Anomala*
4. Larvae found in rotten logs or stumps, sometimes under dried manure, Labrum wider than long; with or without (Fig. 144) two longitudinal rows of spines on radula; setae of lateral margins of labrum of various lengths but not strongly curved (Fig. 44, 50)..... 5
4. Larvae usually formed in sandy soils, labrum (Fig. 50) as long as wide, strongly rounded but asymmetrical; without longitudinal rows of spines on radula; lateral margins of labrum with strongly curved, flattened setae which increase in length distally..... *Cotalpa lanigera*
5. Larvae found in rotten logs or stumps, without two longitudinal rows of spines on radula (Fig. 144); distal sensory area not produced into a single large, chitinous tubercle, without semicircular ring at base (Fig. 44)..... *Pelidnota punctata*
5. Larvae under rotten logs or stumps, or under dried manure on sandy soils; with two longitudinal rows of spines on radula; distal sensory area of epipharynx produced into a single large chitinous tubercle, having between its base and the distal margin a narrow chitinous semicircle..... *Polymoechus brevipēs*

LARVAL KEY TO GENERA OF SUBFAMILY DYNASTINAE

1. With a single ocellar spot at base of antenna..... 2
1. Without an ocellar spot at base of antenna..... 4
2. Radula with a longitudinal cleared area surrounded by recumbent spines similar to other spines of radula, spines not strongly differentiated as in other subfamilies having the double longitudinal row of spines; usually found in manure. . *Ligyrodes (Ligyryus) relictus*
2. Radula without such a longitudinal, non-setose area formed by the absence of spines or setae..... 3
3. Distal sensory area of epipharynx produced into a long, proximal pointing, chitinous process which is curved at its apex, at its base are numerous large setae (Fig. 48, *dsa*); head brownish-tan in color; usually found in burrows near manure..... *Strategus*
3. Distal sensory area of epipharynx not produced into a long, proximal pointing, chitinous process nearly devoid of setae in the region of the distal sensory area (Fig. 151); head nearly black in color, densely punctate; usually found on soil among dead leaves in woods..... *Xyloryctes*
4. Epipharynx with the chitinous portion of the distal sensory area produced to form a single broad tubercle (fig. 45); labrum strongly asymmetrical; sides of labrum strongly rounded; setae of radula very short, not hooked (Fig. 145)..... *Ligyryus gibbosus*
4. Epipharynx with the chitinous portion of the distal sensory area produced to form two tubercles or spines (Fig. 53, 54), labrum more nearly symmetrical; sides of labrum less rounded..... 5
5. Distal sensory area of the epipharynx produced in the form of two broad tubercles close to the distal margin of the labrum (Fig. 54); head and mandibles almost black in color; head strongly punctured; prothorax with a large, brown more heavily chitinized area on the sides which is deeply bipunctate; usually extremely large grubs..... *Dynastes tityrus*
5. Distal sensory area of the epipharynx produced in the form of two small spines and more remote from the distal margin of the labrum (Fig. 53); head yellow in color; sparsely and finely punctate; prothorax without brown, chitinous areas on sides; never extremely large grubs..... *Ochrosidia (Cyclocephala) immaculata*²

² *Dyscinetus* has not been studied. Davis (1916) states that *D. trachypygus* has "a dark brown head which is inconspicuously reticulate and covered with irregularly placed fine punctures, in this respect differing from all species (which he mentions) except *Strategus*, the head of which is much more coarsely punctate and the species is much larger. The ventral surface of the anal segment bears a patch of hooked spines and the upper surface of the same segment is covered, excepting along the median line, with fine hairs, those at the tip being shorter, stouter and more spine-like."

LARVAL KEY TO GENERA OF SUBFAMILY CETONIINAE

1. Labrum almost as long as wide, not distinctly trilobed (Fig. 66); emarginations of labrum relatively shallow; a distinct ocellar spot at base of each antenna; distal sensory area of epipharynx produced into a conspicuous chitinous tubercle; larvae live in wood. *Trichiotinus*
1. Labrum considerably wider than long, distinctly trilobed, relatively deeply emarginate (Fig. 62); no ocellar spot at base of antenna; distal sensory area not produced into a chitinous tubercle; larvae live in various situations, one genus, (*Osmoderma*,) in wood. 2
2. Epipharynx with a chitinous, semicircular carina near distal margin of the median lobe (Fig. 65); proximad of this ridge is a semicircle of about sixteen sensory pores.³ On the side of the epipharynx additional pores apparently make the semicircle continuous almost to the clypeo-labral suture; tarsal claws normal, curved and sharply pointed; larvae live in ant nests. *Cremastocheilus*
2. Epipharynx without a chitinous, semicircular carina on distal margin of median lobe; the median lobe is provided with a conspicuous semicircle of spines (Fig. 68); tarsal claws usually modified into blunt, cylindrical, setaceous tubercles⁴. 3
3. Epipharynx with about ten spines in a semicircular row in distal sensory area; placed somewhat obliquely (Fig. 68); no chitinous sensory tubercle in proximal sensory area near clypeo-labral suture mesad of tormae; larva live in sandy soil (rare) . . . *Stephanucha*
3. Epipharynx usually with more than ten spines (about 15–17) in a semi-circular row in distal sensory area; placed almost transversely; with a well-defined sensory tubercle in proximal sensory area near clypeo-labral suture (Fig. 57, 59); larvae crawl on their backs. 4
4. Radula of last abdominal segment without a longitudinal, double row of mesad pointing spines; larvae live in wood. *Osmoderma eremicola*
4. Radula of last abdominal segment with a longitudinal double row of mesad pointing spines; larvae live in manure or soil that is rich in decaying organic matter. 5
5. Radula of last abdominal segment (Fig. 150) with spines of the longitudinal rows short, separated from each other by a distance nearly equal to the length of the spines; apices of opposing spines distant from each other by less than the length of an individual spine; spines about twice as long as their width at base; antepenultimate antennal segment longer than the terminal segment; usually found in rich, sandy or loam soil. . . . *Cotinis*
5. Radula of last abdominal segment (Fig. 148, 149) with spines of longitudinal rows longer, separated from each other by a distance much less than the length of the spines; apices of opposing spines separated from each other by a distance greater than the length of an individual spine; spines considerably more than twice as long as width at base; antepenultimate antennal segment not longer than the terminal segment, larvae usually found in manure. 6
6. Radula of last abdominal segment with spines of longitudinal rows diverging posteriorly (Fig. 149) *Euphoria sepulchralis*
6. Radula of last abdominal segment with spines of longitudinal rows converging posteriorly (Fig. 148) *Euphoria inda* and *Euphoria fulgida*

LARVAL KEY TO GENERA OF FAMILY LUCANIDAE

1. Antennae five-segmented. 2
1. Antennae four-segmented. 3
2. Dorsal lobe of the three anal lobes acutely pointed on its ventral margin, lateral lobes with

³ In the only specimen available for study the epipharynx is almost devoid of setae but in their place numerous pores are present which may be trichopores whose setae have been lost, or they may, in fact, be sensillia.

⁴ Claws of *Stephanucha* have not been examined.

- a concentric oval line (Fig. 154).....*Dorcus*
- 2. Dorsal lobe of the three anal lobes with its ventral margin strongly rounded; lateral lobes without a concentric oval line.....*Lucanus*
- 3. Caudal region of radula of the last ventral segment with spinose setae; anal opening on each side.....*Platycerus*⁵
- 3. Caudal region of radula without spinose setae (Fig. 153).....4
- 4. Lateral lobes of anus large, subtriangular, not emarginate at their ventral point of union; superior lobe large.....*Ceruchus*
- 4. Lateral lobes of anus plainly elliptical, emarginate at their ventral point of union; superior lobe small (Fig. 153).....*Sinodendron*

ARTIFICIAL KEY TO SOME KNOWN THIRD INSTAR LARVAE OF THE GENUS PHYLLOPHAGA

- 1. Longitudinal rows of radula with less than five spines (usually four in right and three in left row); the tips of opposing spines greatly overlapping, extending almost to the bases of the opposing spines (Southwestern species) (Fig. 157).....*cribrosa* (Lec.)
- 1. Longitudinal rows of radula with more than five spines in each row; the tips of opposing spines never greatly overlapping (excepting *longilarsa* which has 8 to 12 spines).....2
- 2. Each longitudinal row of radular spines composed of a series of spines varying from two rows at the anterior end to three and four rows posteriorly, these compound rows and space between them being rather strongly divergent posteriorly; cephalic spines usually shorter than the caudal spines (Southwestern species) (Fig. 158).....*farcta* (Lec.)
- 2. Each longitudinal row of radular spines composed of a single series of spines, not composed of several rows as in *farcta*, may or may not diverge posteriorly; spines of various lengths.3
- 3. Longitudinal rows with never more than 16 spines in each row, usually less but not fewer than five.....4
- 3. Longitudinal rows with more than 16 spines in a row.....10
- 4. Two rows of longitudinal spines arranged in the form of a distinct oval; with 12-13 spines in each row; spines short, scarcely as long as the distance separating the bases of adjoining spines (Fig. 188).....*iristis* (Fab)
- 4. Two rows of longitudinal spines arranged in nearly parallel rows; with from 5-16 spines in each row; spines variable in length and distance apart.....5
- 5. Majority of spines in each row separated from each other at base by a distance that is less than the length of the individual spines; each row of spines strongly irregular; with 8 to 16 spines in each row.....6
- 5. Majority of spines in each row separated from each other at base by a distance equal to, or greater than the length of the individual spines; each row of spines more nearly regular or parallel; number of spines in each row never more than 14.....7
- 6. Spines 14 to 16 in a row; apices of opposing spines separated by a distance equal to or slightly less than the length of the individual spines; the majority of spines directed cephalo-mesad (Fig. 163).....*gracilis* (Burm.)
- 6. Spines 8-12 in a row; apices of opposing spines extending beyond the meson and overlapping or crossing each other; the majority of spines directed caudo-mesad (Fig. 162).....*longilarsa* (Say)
- 7. Most of the apices of opposing spines separated from each other by a distance equal to or greater than the length of the individual spines; 11 to 13 spines in each row (Fig. 180).....*implicita* (Horn)
- 7. Most of the apices of opposing spines separated from each other by a distance less than the length of the individual spines.....8

⁵ Genus not seen. The characters given above are from Perris (1877) after Mulsant.

8. Most of the apices of opposing spines reaching the meson and very narrowly separated from each other; 12–13 spines in each row (Fig. 171) *vehemens* (Horn)
8. Most of the apices of opposing spines not reaching the meson with the opposing apices more widely separated from each other; 13–14 spines in each row 9
9. Spines shorter, much less than half the length of the distance separating the majority of adjacent spines at their base; 13 spines in each row (Fig. 156) *lanceolata* (Say)
9. Spines longer, usually greater than half the length of the distance separating the majority of adjacent spines at their base; 14 spines in each row (Fig. 175) *drakei* (Kby.)
10. Spines of radular rows not stout; individual spines usually equal in length or shorter than the intervening distance between the bases of adjacent spines; the bases of the spines much narrower than the interval between the spines 11
10. Spines of radular rows usually stout; individual spines in most instances much longer than the intervening distance between the bases of adjacent spines; in many species the bases of the spines are wider than the interval between the adjacent spines 18
11. Apices of most of the opposing spines meeting, or slightly overlapping each other, on the meson; 19–22 spines in each row; a conspicuous transverse row of setae between the radular spines and the anal opening (Fig. 161) *ephilida* (Say)
11. Apices of most of the opposing spines not meeting on the meson, the tips of opposing spines being separated from each other by a distance equal to or greater than the length of the individual spines; 19–29 spines in each row; no conspicuous transverse row of setae between the radular spines and the anal opening 12
12. Spines of radula arranged in nearly parallel rows; 29 spines in left row, 25 in right row; spines short, scarcely longer than their width at base (Fig. 173) *horni* (Smith)
12. Spines of radular rows arranged in more irregularly parallel rows, no rows with more than 27 spines; most spines considerably longer than their width at base 13
13. Longitudinal rows with from 25 to 27 spines 14
13. Longitudinal rows with from 17 to 21 spines 15
14. Rows of spines very irregularly parallel: with 25 spines in right row and 27 in left row; spines about equal in length to the distance between adjacent bases (Fig. 189) *inversa* (Horn)
14. Rows of spines more regularly parallel; with 26 spines in each row; spines usually shorter than the distance between adjacent bases (Fig. 160) *latifrons* (Lec)
15. Radular rows of spines diverging anteriorly 16
15. Radular rows of spines not diverging anteriorly 17
16. Radular rows of spines approximate at caudal ends (distance between opposing apices of caudal spines less than the length of the spines); 19 to 20 spines in each row (Fig. 183) *delata* (Horn)
16. Radular rows of spines less approximate at caudal ends of rows (distance between opposing apices of caudal spines at least equal to or greater than the length of the spines); 17 to 19 spines in each row (Fig. 172) *fusca* (Froel.)
17. With 19 to 21 spines in each longitudinal row; the two rows constricted at middle^a (Fig. 176) *marginalis* (Lec.)
17. With 18 spines in each longitudinal row; the two rows not constricted at middle (Fig. 174) *fervida* (Fab.)
18. Spines of radular rows short, scarcely longer than the intervening spaces at their bases; the rows of spines strongly diverging caudally then converging near their caudal ends . 19
18. Spines of radular rows considerably longer than the intervening spaces at their bases; not strongly divergent but in a few species becoming gradually curved near caudal ends 20

^a In the single third instar of this species studied this constriction appears but this may be an abnormality since several second instar grubs available do not show this constriction.

19. Spines of radular rows strongly divergent before the middle; rows not meeting at their anterior and posterior ends; with 23 spines in each row (Fig. 186).....*vetula* (Horn)
19. Spines of radular rows becoming suddenly strongly divergent at or behind middle; rows meeting at anterior end; left row with a conspicuous interval devoid of spines; with 27 and 28 spines in the rows (Fig. 167).....*calceata* (Lec.)
20. Rows nearly parallel; apices of most opposing spines separated by a distance less than the length of the spines (Fig. 164).....*futilis* (Lec.)
20. Rows more or less parallel or gradually curving; apices of the majority of opposing spines separated by a distance equal to or greater than the length of the spines.....21
21. Rows short, occupying less than half the distance between the anal opening and the anterior margin of the segment; spines regularly placed and rows slightly curving near caudal end; 20 to 22 spines per row (Fig. 187).....*affabilis* (Horn)
21. Rows longer, occupying one-half or more of the distance between the anal opening and the anterior margin of the segment; spines of varying arrangement; usually, but not always, with more than 22 spines per row.....22
22. Spines short, not more than twice as long as width at base.....23
22. Majority of spines considerably more than twice as long as width at base.....25
23. Spines of uniform size and length, rows more regularly spaced and gradually curving outward at center and approaching one another at each end; with 24 spines in one row and 29 in the other (Fig. 177).....*fraterna* Harris
23. Spines not of uniform size and length, rows more irregularly spaced and not gradually curving outward; with not less than 27 spines in any row.....24
24. Rows of spines nearly parallel, but with rather jagged rows not noticeably approaching each other at the ends; with 27 in one row and 29 in another (Fig. 165)..*prunina* (Lec.)
24. Rows of spines not parallel, slightly curving and approaching each other at caudal end; with 33 spines in one row and 32 in another (Fig. 184).....*ilicis* (Knoch)
25. Rows strongly curved anteriorly to form a rounded cephalic end composed of smaller spines, one row with 24 spines, the other with 28 spines leaving two conspicuous spines at caudal end with no spines opposing them in the other row (Fig. 185).....*crenulata* (Froel.)
25. Rows not conspicuously rounded at anterior end; without unopposed spines at caudal end of one row.....26
26. Rows of spines longer, with 32 spines in one row and 31 in the other (Fig. 179).....*profunda* (Blanch.)
26. Rows of spines shorter, with less than 30 spines in any row.....27
27. Spines irregularly placed, forming jagged rows.....28
27. Spines regularly placed, forming more even rows.....30
28. Three caudal spines of each row not more than half as long as the majority of the spines cephalad of them: with 25 spines in one row and 24 in the other (Fig. 181)..*balia* (Say)
28. Three caudal spines not differing greatly in length from the cephalic ones.....29
29. With 27 spines in each row (Fig. 166).....*congrua* (Lec.)
29. With 25 spines in one row and 26 in the other (Fig. 168).....*crassissima* (Blanch.)
30. With both rows of spines bent or constricted mesally near the middle of the rows, 29 spines in each row (Fig. 182).....*hirticula* (Knoch.)
30. With not more than one, or none, of the rows constricted near the middle of the row; not more than 26 spines in each row.....31
31. Apices of most of the opposing spines widely separated, being nearly twice the length of the spines apart.....32
31. Apices of most of the opposing spines not as widely separated, being considerably less than twice the length of the spines apart.....33
32. With the right row of spines constricted or bent near its middle; 28 spines in one row and 24 in the other (Fig. 178).....*corrosa* (Lec.)

32. With neither row of spines constricted or bent near the middle; 23 spines in one row and 20 in the other (Fig. 159)..... *torta* (Iec.)
33. Rows of spines rather regularly curved throughout; with 22 spines in one row and 25 in the other (Fig. 170)..... *micans* (Knöck)
33. Rows of spines somewhat bulging behind the center; with 24 spines in one row and 26 in the other (Fig. 169)..... *bipartita* (Horn)

SUMMARY

The foregoing study of the larvae of North American Lamellicornia, including the now recognized families—Scarabaeidae, Lucanidae, Trogidae, and Passalidae—attempts to bring together our knowledge of their biology, including the writer's life-history studies, and presents keys for their identification based on morphological studies. No comparative studies of the structural characters of these insects have hitherto been attempted, and it is hoped that this work, though far from being complete, will afford a stepping-stone to further progress in our knowledge of the group.

For taxonomic purposes the characters of the mouthparts and the last abdominal segment have proved the most useful. The analytical keys can be considered only preliminary, inasmuch as a great many of our species are still unknown in the larval stage. The long life-cycle in many species makes rearing very difficult.

In the discussion given to biology, there have been brought together, in a comparative way, the more general facts concerning postembryonic development. Some consideration is given to the late embryonic processes, and larval development is considered in a general way, as is also pupal development. This is followed by more-detailed life-history studies in the sub-families Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, and the coprophagous species of the family Scarabaeidae.

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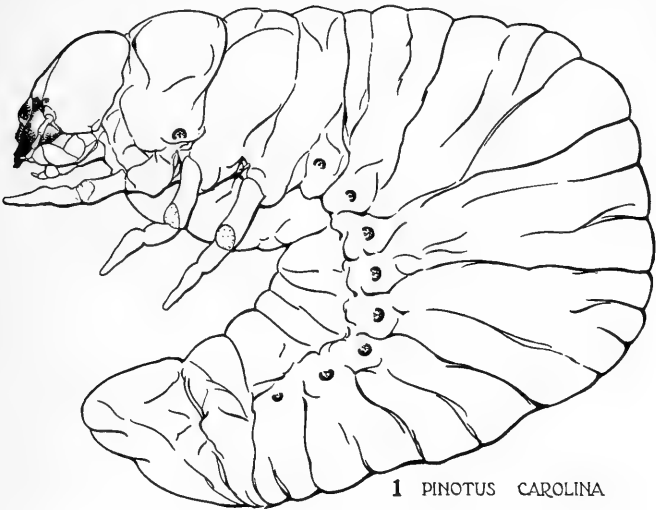
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PLATE I

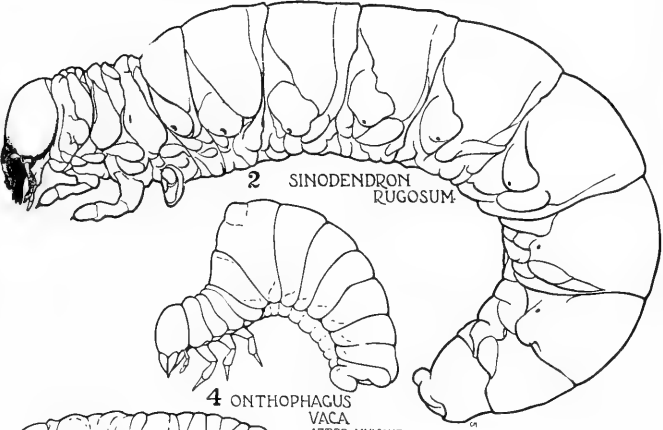
EXPLANATION OF PLATE I

LATERAL ASPECTS OF THE LARVAE OF SCARABAEOIDEA

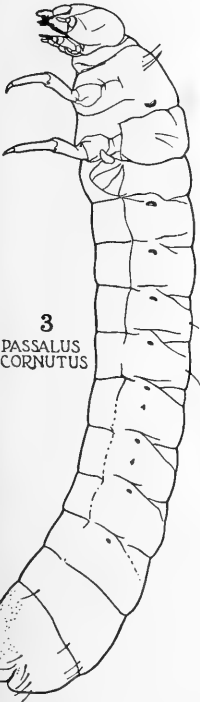
- Fig. 1. *Pinotus carolina*.
Fig. 2. *Sinodendron rugosum*.
Fig. 3. *Passalus cornutus*.
Fig. 4. *Onthophagus vaca* (after Mulsant).
Fig. 5. *Amphicoma* sp.
Fig. 6. *Aphodius* sp. (probably *finetarius*).



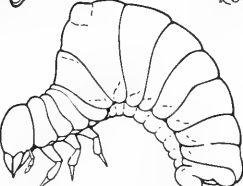
1 PINOTUS CAROLINA



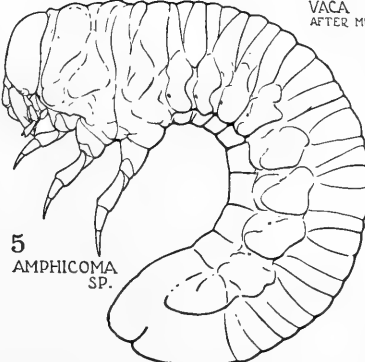
2 SINODENDRON
RUGOSUM



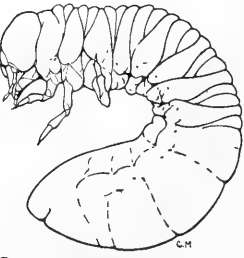
3 PASSALUS
CORNUTUS



4 ONTHOPAGUS
VACCA
AFTER MULSANT



5 AMPHICOMA
SP.



6 APHODIUS SP.

THE
OF THE
OF THE

PLATE II

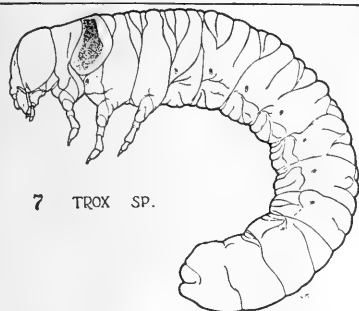
EXPLANATION OF PLATE II

LATERAL ASPECTS OF THE LARVAE OF SCARABAEOIDEA

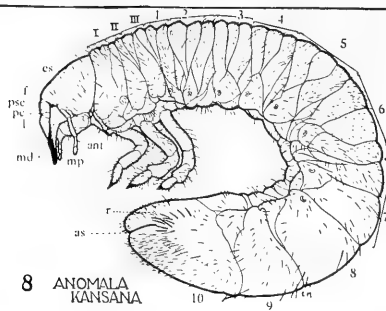
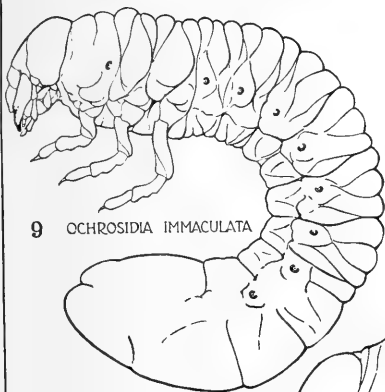
- Fig. 7. *Trox* sp.
 Fig. 8. *Anomala kansana*.
 Fig. 9. *Ochrosidia immaculata*.
 Fig. 10. *Ligyrrus gibbosus*.
 Fig. 11. *Euphoria inda*.
 Fig. 12. *Phyllophaga crassissima*.

ABBREVIATIONS EMPLOYED

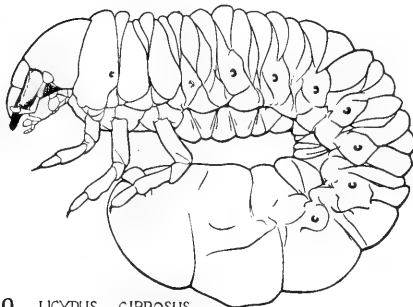
<i>ant</i>	antenna	<i>pc</i>	preclypeus
<i>as</i>	anal slit	<i>pse</i>	postclypeus
<i>es</i>	epicranial suture	<i>r</i>	radula
<i>f</i>	front	I	prothorax
<i>l</i>	labrum	II	mesothorax
<i>md</i>	mandible	III	metathorax
<i>mp</i>	maxillary palpus	1-10	abdominal segments



7 TROX SP.

8 ANOMALA
KANSANA

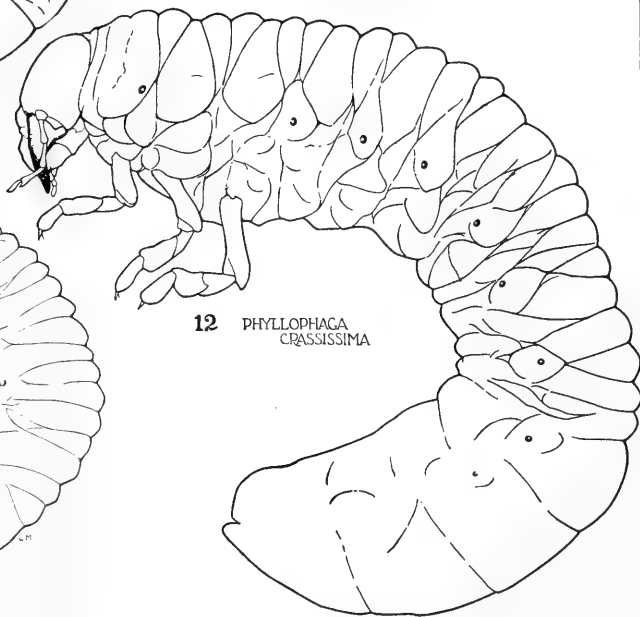
9 OCHROSIDIA IMMACULATA



10 LIGYRUS GIBBOSUS



11 EUPHORIA INDA



12 PHYLLOPHAGA
CRASSISSIMA

11/11/11 11:11 AM

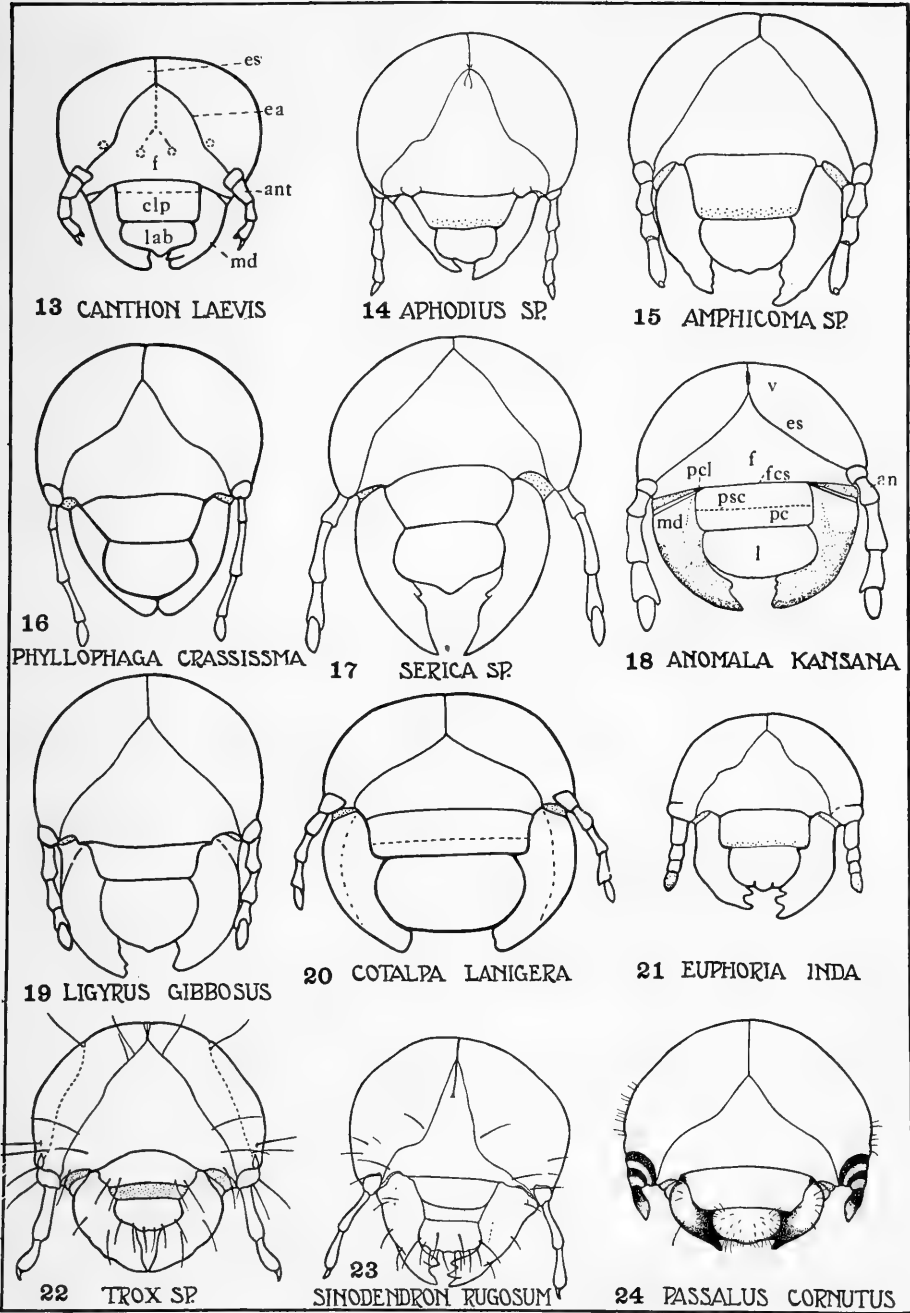
PLATE III

EXPLANATION OF PLATE III
CEPHALIC ASPECT OF THE LARVAL HEADS

- Fig. 13. *Canthon laevis*.
Fig. 14. *Aphodius sp.*
Fig. 15. *Amphicoma sp.*
Fig. 16. *Phyllophaga crassissima*.
Fig. 17. *Serica sp.*
Fig. 18. *Anomala kansana*.
Fig. 19. *Ligyris gibbosus*.
Fig. 20. *Cotalpa lanigera*.
Fig. 21. *Euphoria inda*.
Fig. 22. *Trox sp.*
Fig. 23. *Sinodendron rugosum*.
Fig. 24. *Passalus cornutus*.

ABBREVIATIONS EMPLOYED

<i>ant</i>	antenna	<i>md</i>	mandible
<i>ea</i>	epicranial arm	<i>pc</i>	preclypeus
<i>es</i>	epicranial suture	<i>pcl</i>	precoila
<i>f</i>	front	<i>pse</i>	postclypeus
<i>fcs</i>	fronto-clypeal suture	<i>v</i>	vertex
<i>l</i> or <i>lab</i>	labrum		



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PLATE IV

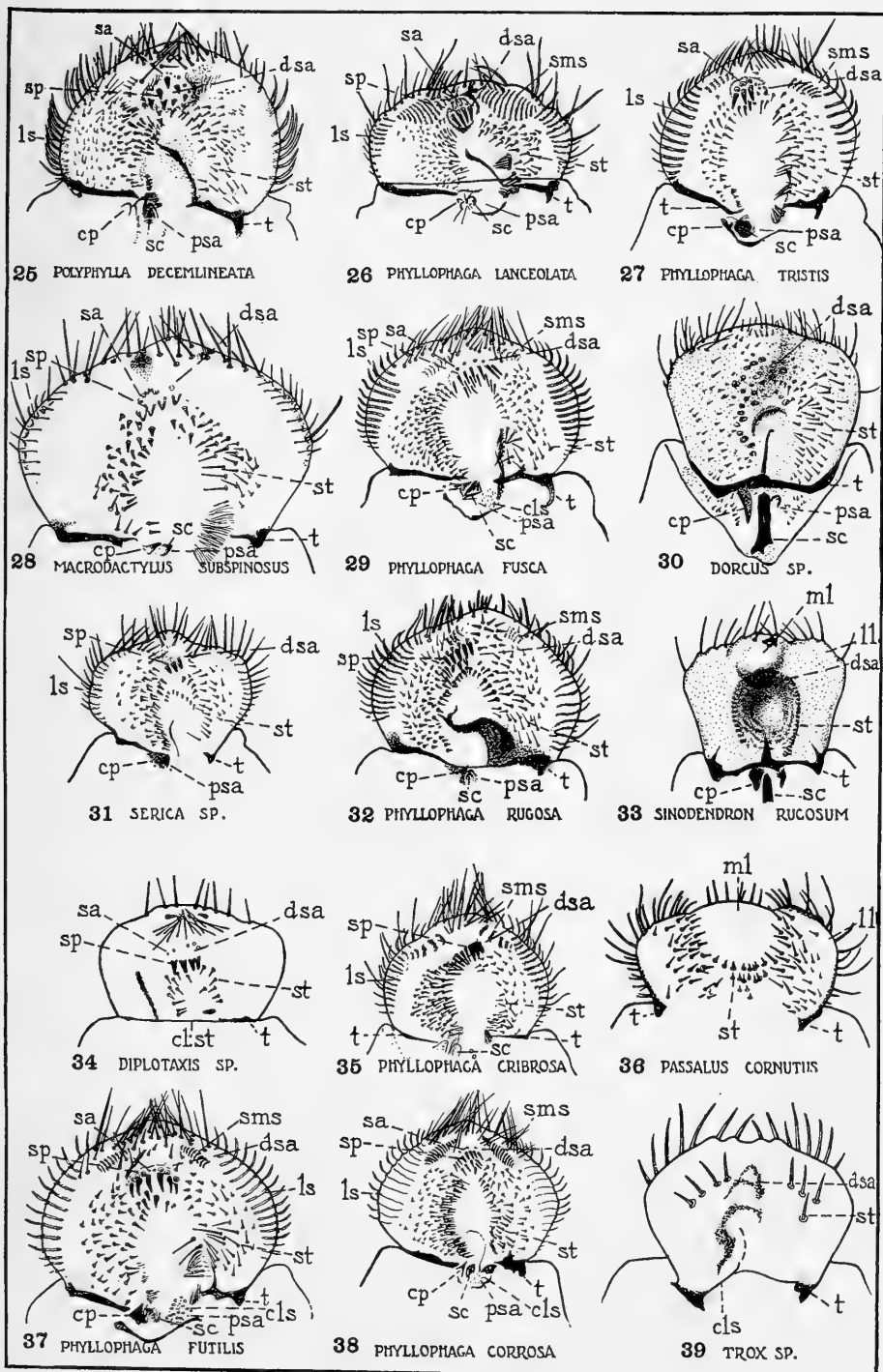
EXPLANATION OF PLATE IV

EPIPHARYNX

- Fig. 25. *Polyphylla decemlineata*.
 Fig. 26. *Phyllophaga lanceolata*.
 Fig. 27. *Phyllophaga tristis*.
 Fig. 28. *Macroductylus subspinosus*.
 Fig. 29. *Phyllophaga fusca*.
 Fig. 30. *Dorcus sp.*
 Fig. 31. *Serica sp.*
 Fig. 32. *Phyllophaga rugosa*.
 Fig. 33. *Sinodendron rugosum*.
 Fig. 34. *Diplotaxis sp.*
 Fig. 35. *Phyllophaga cribrrosa*.
 Fig. 36. *Passalus cornutus*.
 Fig. 37. *Phyllophaga futilis*.
 Fig. 38. *Phyllophaga corrosa*.
 Fig. 39. *Trox sp.*

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setae
<i>ml</i>	median lobe	<i>t</i>	torma



1. The first part of the paper is devoted to the study of the properties of the function $f(x)$ defined by the equation

PLATE V

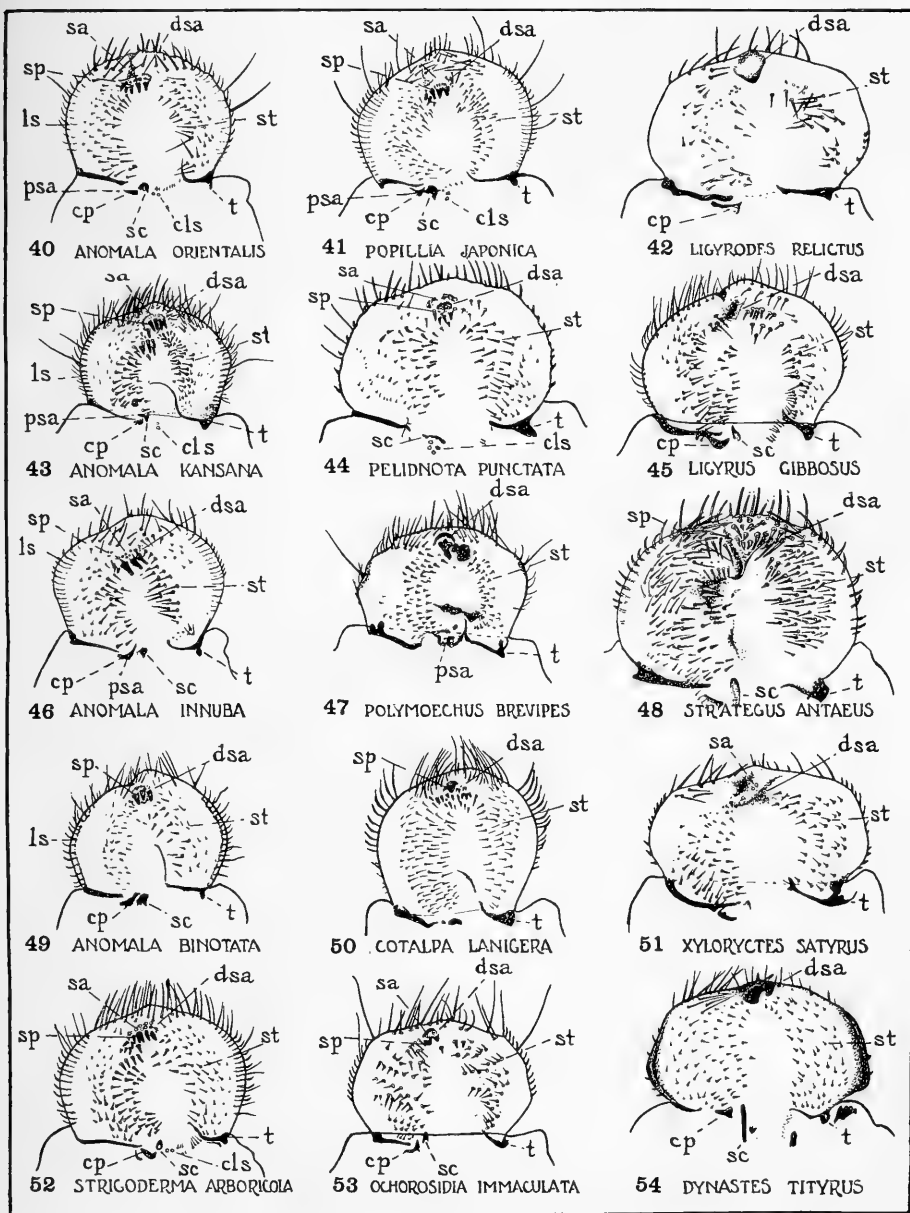
EXPLANATION OF PLATE V

EPIPHARYNX

- Fig. 40. *Anomala orientalis*.
 Fig. 41. *Popillia japonica*.
 Fig. 42. *Ligyrodes relictus*.
 Fig. 43. *Anomala kansana*.
 Fig. 44. *Pelidnota punctata*.
 Fig. 45. *Ligyryus gibbosus*.
 Fig. 46. *Anomala innuba*.
 Fig. 47. *Polymoechus brevipes*.
 Fig. 48. *Strategus antaeus*.
 Fig. 49. *Anomala binotata*.
 Fig. 50. *Cotalpa lanigera*.
 Fig. 51. *Xyloryctes satyrus*.
 Fig. 52. *Strigoderma arboricola*.
 Fig. 53. *Ochrosidia immaculata*.
 Fig. 54. *Dynastes tityrus*.

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense-cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setae
<i>ml</i>	median lobe		torma



DATE _____

1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021, 2022, 2023, 2024, 2025, 2026, 2027, 2028, 2029, 2030, 2031, 2032, 2033, 2034, 2035, 2036, 2037, 2038, 2039, 2040, 2041, 2042, 2043, 2044, 2045, 2046, 2047, 2048, 2049, 2050, 2051, 2052, 2053, 2054, 2055, 2056, 2057, 2058, 2059, 2060, 2061, 2062, 2063, 2064, 2065, 2066, 2067, 2068, 2069, 2070, 2071, 2072, 2073, 2074, 2075, 2076, 2077, 2078, 2079, 2080, 2081, 2082, 2083, 2084, 2085, 2086, 2087, 2088, 2089, 2090, 2091, 2092, 2093, 2094, 2095, 2096, 2097, 2098, 2099, 2100, 2101, 2102, 2103, 2104, 2105, 2106, 2107, 2108, 2109, 2110, 2111, 2112, 2113, 2114, 2115, 2116, 2117, 2118, 2119, 2120, 2121, 2122, 2123, 2124, 2125, 2126, 2127, 2128, 2129, 2130, 2131, 2132, 2133, 2134, 2135, 2136, 2137, 2138, 2139, 2140, 2141, 2142, 2143, 2144, 2145, 2146, 2147, 2148, 2149, 2150, 2151, 2152, 2153, 2154, 2155, 2156, 2157, 2158, 2159, 2160, 2161, 2162, 2163, 2164, 2165, 2166, 2167, 2168, 2169, 2170, 2171, 2172, 2173, 2174, 2175, 2176, 2177, 2178, 2179, 2180, 2181, 2182, 2183, 2184, 2185, 2186, 2187, 2188, 2189, 2190, 2191, 2192, 2193, 2194, 2195, 2196, 2197, 2198, 2199, 2200, 2201, 2202, 2203, 2204, 2205, 2206, 2207, 2208, 2209, 2210, 2211, 2212, 2213, 2214, 2215, 2216, 2217, 2218, 2219, 2220, 2221, 2222, 2223, 2224, 2225, 2226, 2227, 2228, 2229, 2230, 2231, 2232, 2233, 2234, 2235, 2236, 2237, 2238, 2239, 2240, 2241, 2242, 2243, 2244, 2245, 2246, 2247, 2248, 2249, 2250, 2251, 2252, 2253, 2254, 2255, 2256, 2257, 2258, 2259, 2260, 2261, 2262, 2263, 2264, 2265, 2266, 2267, 2268, 2269, 2270, 2271, 2272, 2273, 2274, 2275, 2276, 2277, 2278, 2279, 2280, 2281, 2282, 2283, 2284, 2285, 2286, 2287, 2288, 2289, 2290, 2291, 2292, 2293, 2294, 2295, 2296, 2297, 2298, 2299, 2300, 2301, 2302, 2303, 2304, 2305, 2306, 2307, 2308, 2309, 2310, 2311, 2312, 2313, 2314, 2315, 2316, 2317, 2318, 2319, 2320, 2321, 2322, 2323, 2324, 2325, 2326, 2327, 2328, 2329, 2330, 2331, 2332, 2333, 2334, 2335, 2336, 2337, 2338, 2339, 2340, 2341, 2342, 2343, 2344, 2345, 2346, 2347, 2348, 2349, 2350, 2351, 2352, 2353, 2354, 2355, 2356, 2357, 2358, 2359, 2360, 2361, 2362, 2363, 2364, 2365, 2366, 2367, 2368, 2369, 2370, 2371, 2372, 2373, 2374, 2375, 2376, 2377, 2378, 2379, 2380, 2381, 2382, 2383, 2384, 2385, 2386, 2387, 2388, 2389, 2390, 2391, 2392, 2393, 2394, 2395, 2396, 2397, 2398, 2399, 2400, 2401, 2402, 2403, 2404, 2405, 2406, 2407, 2408, 2409, 2410, 2411, 2412, 2413, 2414, 2415, 2416, 2417, 2418, 2419, 2420, 2421, 2422, 2423, 2424, 2425, 2426, 2427, 2428, 2429, 2430, 2431, 2432, 2433, 2434, 2435, 2436, 2437, 2438, 2439, 2440, 2441, 2442, 2443, 2444, 2445, 2446, 2447, 2448, 2449, 2450, 2451, 2452, 2453, 2454, 2455, 2456, 2457, 2458, 2459, 2460, 2461, 2462, 2463, 2464, 2465, 2466, 2467, 2468, 2469, 2470, 2471, 2472, 2473, 2474, 2475, 2476, 2477, 2478, 2479, 2480, 2481, 2482, 2483, 2484, 2485, 2486, 2487, 2488, 2489, 2490, 2491, 2492, 2493, 2494, 2495, 2496, 2497, 2498, 2499, 2500, 2501, 2502, 2503, 2504, 2505, 2506, 2507, 2508, 2509, 2510, 2511, 2512, 2513, 2514, 2515, 2516, 2517, 2518, 2519, 2520, 2521, 2522, 2523, 2524, 2525, 2526, 2527, 2528, 2529, 2530, 2531, 2532, 2533, 2534, 2535, 2536, 2537, 2538, 2539, 2540, 2541, 2542, 2543, 2544, 2545, 2546, 2547, 2548, 2549, 2550, 2551, 2552, 2553, 2554, 2555, 2556, 2557, 2558, 2559, 2560, 2561, 2562, 2563, 2564, 2565, 2566, 2567, 2568, 2569, 2570, 2571, 2572, 2573, 2574, 2575, 2576, 2577, 2578, 2579, 2580, 2581, 2582, 2583, 2584, 2585, 2586, 2587, 2588, 2589, 2590, 2591, 2592, 2593, 2594, 2595, 2596, 2597, 2598, 2599, 2600, 2601, 2602, 2603, 2604, 2605, 2606, 2607, 2608, 2609, 2610, 2611, 2612, 2613, 2614, 2615, 2616, 2617, 2618, 2619, 2620, 2621, 2622, 2623, 2624, 2625, 2626, 2627, 2628, 2629, 2630, 2631, 2632, 2633, 2634, 2635, 2636, 2637, 2638, 2639, 2640, 2641, 2642, 2643, 2644, 2645, 2646, 2647, 2648, 2649, 2650, 2651, 2652, 2653, 2654, 2655, 2656, 2657, 2658, 2659, 2660, 2661, 2662, 2663, 2664, 2665, 2666, 2667, 2668, 2669, 2670, 2671, 2672, 2673, 2674, 2675, 2676, 2677, 2678, 26

PLATE VI

EXPLANATION OF PLATE VI

EPIPHARYNX

- Fig. 55. *Canthon laevis*.
 Fig. 56. *Aphodius* sp.
 Fig. 57. *Euphoria fulgida*.
 Fig. 58. *Geotrupes stercorarius*. (after Schiödte)
 Fig. 59. *Cotinis nitida*.
 Fig. 60. *Euphoria sepulchralis*.
 Fig. 61. *Amphicoma* sp.
 Fig. 62. *Osmoderma eremicola*.
 Fig. 63. *Euphoria inda*.
 Fig. 64. *Copris tullius*.
 Fig. 65. *Cremastocheilus* sp.
 Fig. 66. *Trichiotinus piger*.
 Fig. 67. *Onthophagus* sp.
 Fig. 68. *Stephanucha pilipennis*.
 Fig. 69. *Phyllophaga futilis*. sense cone

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense-cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setae
<i>ml</i>	median lobe		torma

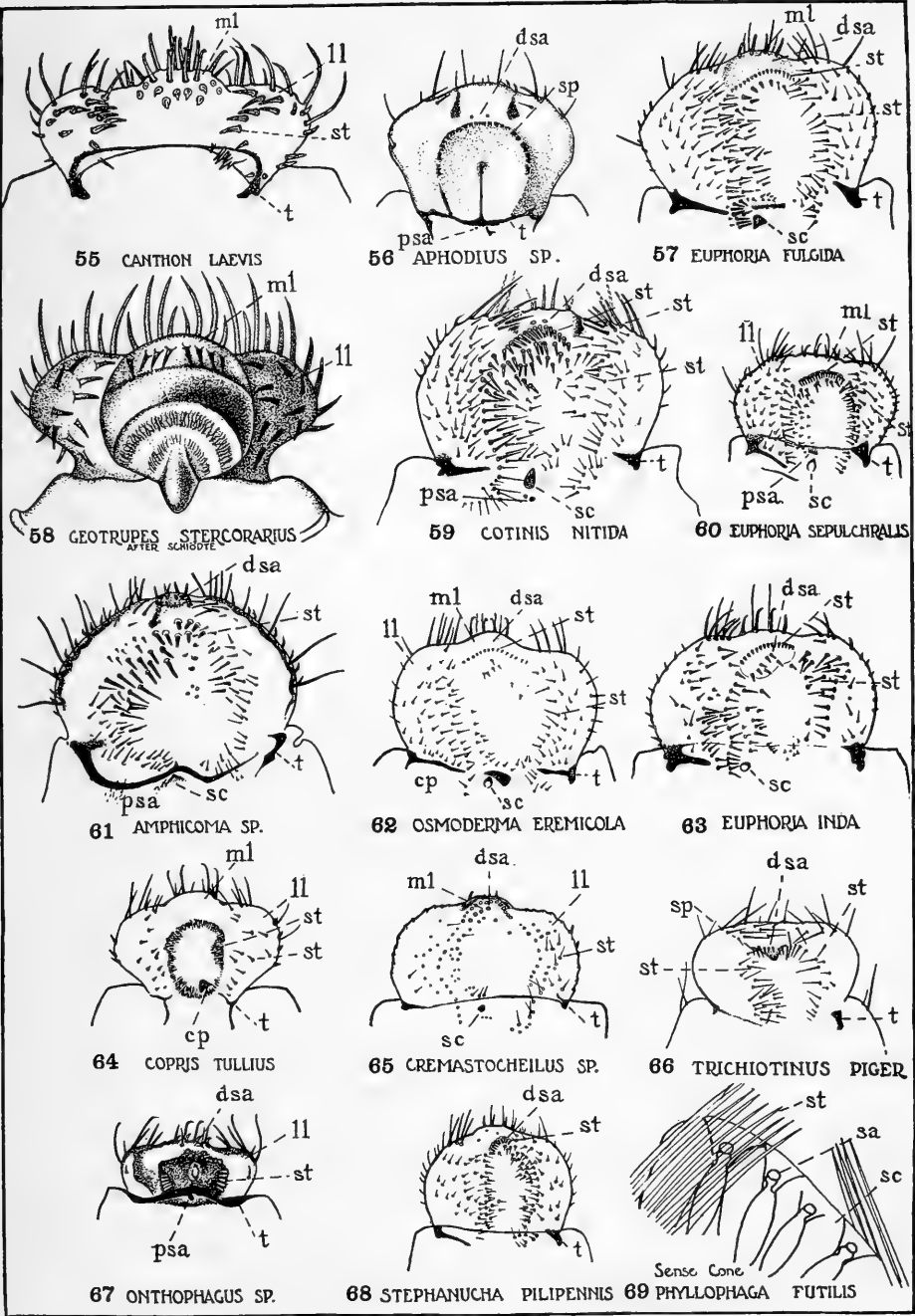


PLATE VII

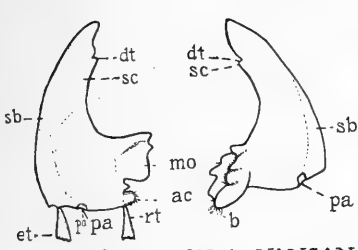
EXPLANATION OF PLATE VII

RIGHT AND LEFT MANDIBLES.—CEPHALIC ASPECT

- Fig. 70. *Anomala kansana*.
 Fig. 71. *Aphodius fimetarius*.
 Fig. 72. *Stephanucha pilipennis*.
 Fig. 73. *Euphoria inda*.
 Fig. 74. *Cotalpa lanigera*.
 Fig. 75. *Ligyris gibbosus*.
 Fig. 76. *Phyllophaga crassissima*.
 Fig. 77. Mandibular articulation.
 Fig. 78. *Canthon laevis*.
 Fig. 79. *Passalus cornutus*.
 Fig. 80. *Sinodendron rugosum*.

ABBREVIATIONS EMPLOYED

<i>ac</i>	acia	<i>pa</i>	preartis
<i>b</i>	brustia	<i>pcl</i>	precoila
<i>dt</i>	dentes	<i>rt</i>	rectotendon
<i>et</i>	extensotendon	<i>sb</i>	scrobe
<i>mo</i>	molar area	<i>sc</i>	scissorial area



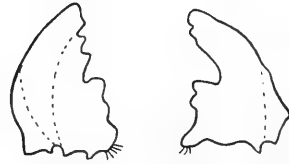
70 ANOMALA KANSANA



71 APHODIUS FIMETARIUS



72 STEPHANUCHA PILIPENNIS



73 EUPHORIA INDA



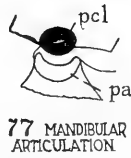
74 COTALPA LANIGERA



75 LIGYRUS GIBBOSUS



76 PHYLLOPHAGA CRASSISSIMA



77 MANDIBULAR
ARTICULATION



78 CANTHON LAEVIS



79 PASSALUS CORNUTUS



80 SINODENDRON RUGOSUM

UNIVERSITY OF WASHINGTON

PLATE VIII

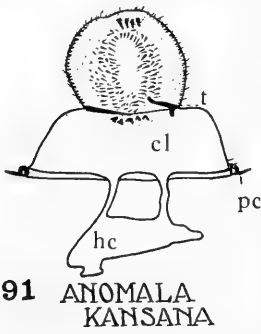
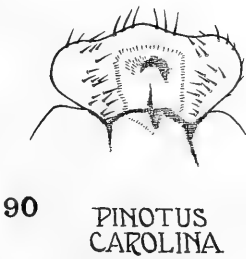
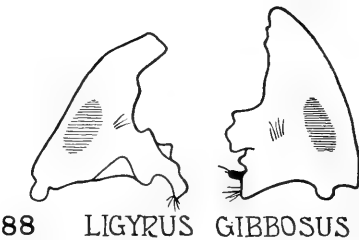
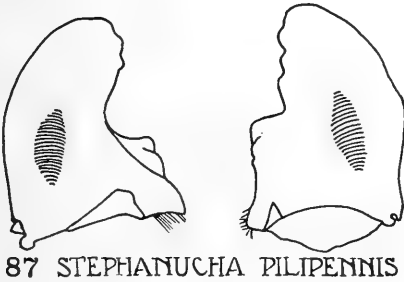
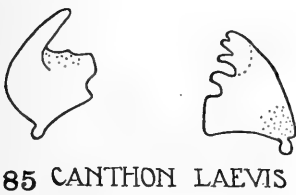
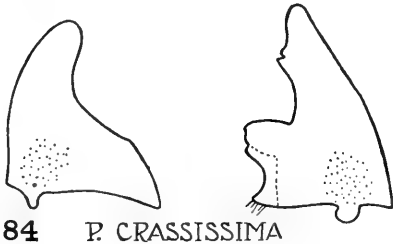
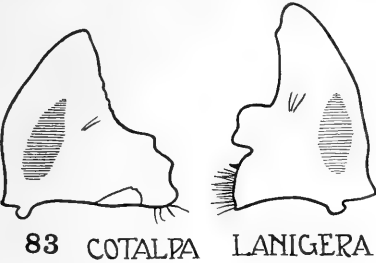
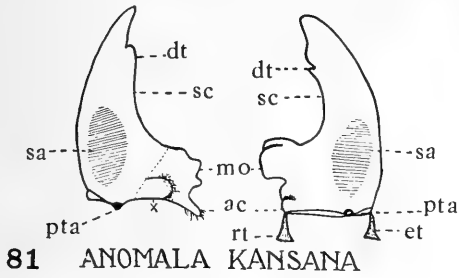
EXPLANATION OF PLATE VIII

RIGHT AND LEFT MANDIBLES—CAUDAL ASPECT AND EPIPHARYNX

- Fig. 81. *Anomala kansana*.
 Fig. 82. *Euphoria inda*.
 Fig. 83. *Cotalpa lanigera*.
 Fig. 84. *Phyllophaga crassissima*.
 Fig. 85. *Canthon laevis*.
 Fig. 86. *Amphicoma* sp.
 Fig. 87. *Stephanucha pilipennis*.
 Fig. 88. *Ligyryus gibbosus*.
 Fig. 89. *Passalus cornutus*.
 Fig. 90. *Pinotus carolina*. Epipharynx.
 Fig. 91. *Anomala kansana*. Showing connection of epipharynx and hypopharynx.

ABBREVIATIONS EMPLOYED

<i>ac</i>	acia	<i>pc</i>	precoila
<i>cl</i>	clypeus	<i>pla</i>	postartis
<i>dt</i>	dentes	<i>rt</i>	rectotendon
<i>et</i>	extensotendon	<i>sa</i>	stridulating area
<i>hc</i>	hypopharyngeal chitinization	<i>sc</i>	scissorial area
<i>mo</i>	molar area	<i>t</i>	torma



UNIVERSITY OF ILLINOIS

PLATE IX

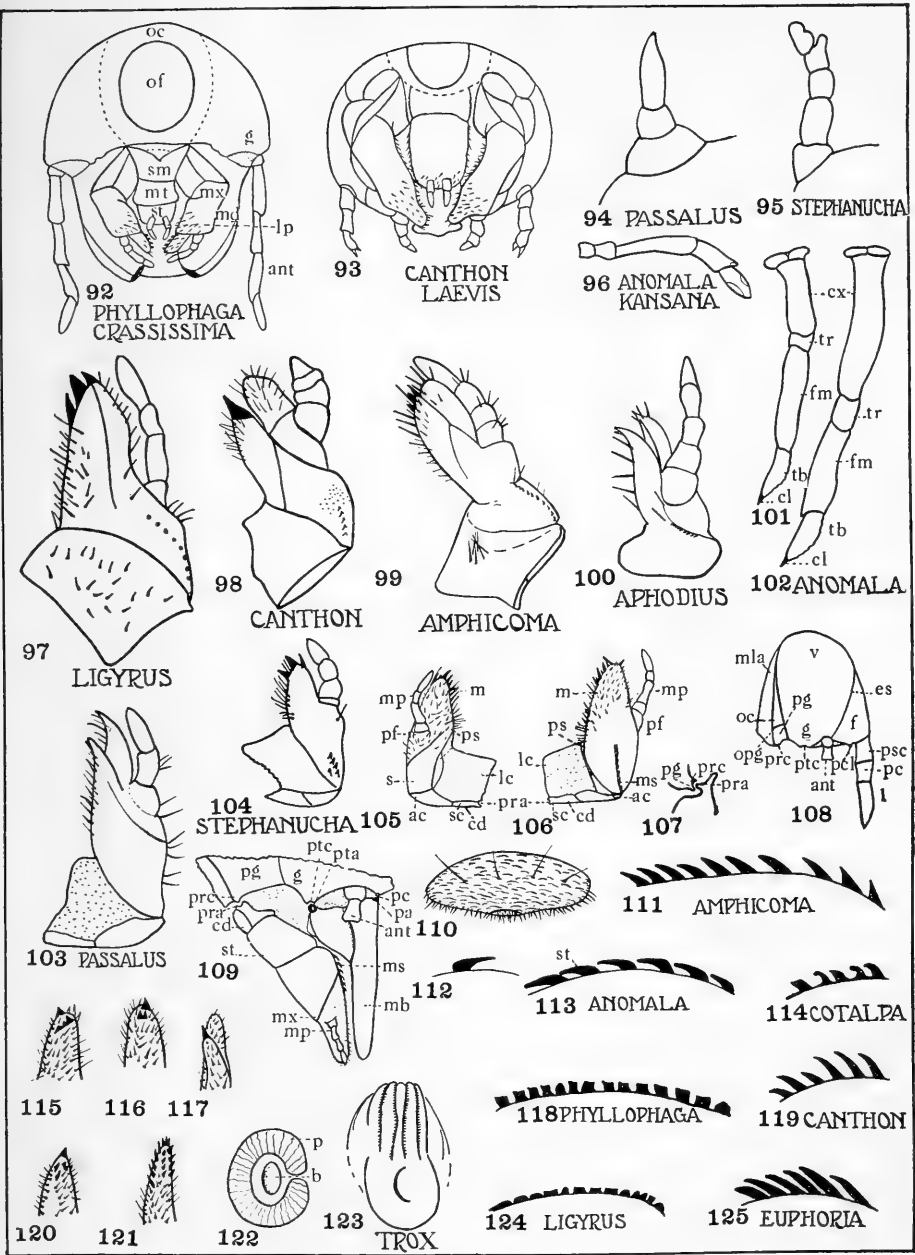
EXPLANATION OF PLATE IX

CAUDAL AND LATERAL ASPECTS OF HEAD; ANTENNAE, MAXILLAE AND PARTS, SPIRACLES, LEGS

- Fig. 92. *Phyllophaga crassissima*. Caudal aspect of the head.
 Fig. 93. *Canthon laevis*. Caudal aspect of the head.
 Fig. 94. *Passalus cornutus*. Antenna.
 Fig. 95. *Stephanucha pilipennis*. Antenna.
 Fig. 96. *Anomala kansana*. Antenna.
 Fig. 97. *Ligyryus gibbosus*. Cephalic aspect of right maxilla.
 Fig. 98. *Canthon laevis*. Cephalic aspect of right maxilla.
 Fig. 99. *Amphicoma* sp. Cephalic aspect of right maxilla.
 Fig. 100. *Aphodius* sp. Cephalic aspect of right maxilla.
 Fig. 101. *Anomala kansana*. Prothoracic leg.
 Fig. 102. *Anomala kansana*. Metathoracic leg.
 Fig. 103. *Passalus cornutus*. Cephalic aspect of right maxilla.
 Fig. 104. *Stephanucha pilipennis*. Cephalic aspect of right maxilla.
 Fig. 105. *Anomala kansana*. Caudal aspect of right maxilla.
 Fig. 106. *Anomala kansana*. Cephalic aspect of right maxilla.
 Fig. 107. *Anomala kansana*. Articulation of maxilla and postgena.
 Fig. 108. *Anomala kansana*. Lateral aspect of the head.
 Fig. 109. Articulation of mandible and maxillae with head capsule.
 Fig. 110. *Anomala kansana*. Labrum.
 Fig. 111. *Amphicoma* sp. Stridulating teeth of right maxilla.
 Fig. 112. *Anomala kansana*. Stridulating tooth of left maxilla.
 Fig. 113. *Anomala kansana*. Stridulating teeth of right maxilla.
 Fig. 114. *Cotalpa lanigera*. Stridulating teeth of right maxilla.
 Fig. 115. *Ligyryus gibbosus*. Mesal aspect of fused galea and lacinia.
 Fig. 116. *Cotalpa lanigera*. Mesal aspect of fused galea and lacinia.
 Fig. 117. *Canthon laevis*. Mesal aspect of divided galea and lacinia.
 Fig. 118. *Phyllophaga crassissima*. Stridulating teeth of right maxilla.
 Fig. 119. *Canthon laevis*. Stridulating teeth of right maxilla.
 Fig. 120. *Euphoria inda*. Mesal aspect of fused galea and lacinia.
 Fig. 121. *Phyllophaga crassissima*. Mesal aspect of fused galea and lacinia.
 Fig. 122. *Anomala kansana*. Left prothoracic spiracle.
 Fig. 123. *Trox* sp. Left prothoracic spiracle.
 Fig. 124. *Ligyryus gibbosus*. Stridulating teeth of right maxilla.
 Fig. 125. *Euphoria inda*. Stridulating teeth of right maxilla.

ABBREVIATIONS EMPLOYED

<i>ac</i>	alacardo	<i>of</i>	occipital foramen
<i>ant</i>	antenna	<i>opg</i>	occipito-postgenal suture
<i>cd</i>	cardo	<i>pa</i>	preartis
<i>cl</i>	claw	<i>pc</i>	preclypeus
<i>cx</i>	coxa	<i>pcl</i>	precoilla
<i>es</i>	epicranial suture	<i>pf</i>	pālpifer
<i>f</i>	front	<i>pg</i>	postgena
<i>fm</i>	femur	<i>pra</i>	parartis
<i>g</i>	gena	<i>prc</i>	paracoilla
<i>l</i>	labrum	<i>ps</i>	parastipes or subgalea
<i>lc</i>	labacoria	<i>psc</i>	postclypeus
<i>lp</i>	labial palpus	<i>pla</i>	postartis
<i>m</i>	mala	<i>plc</i>	postcoilla
<i>md</i>	mandible	<i>s</i>	stipes
<i>mā</i>	maxillaria or maxillary pleurite	<i>sc</i>	subcardo
<i>mp</i>	maxillary palpus	<i>sm</i>	submentum
<i>ms</i>	maxillary scraper	<i>st</i>	stridulating tooth
<i>mt</i>	mentum	<i>th</i>	terbio-tarsus
<i>mx</i>	maxilla	<i>tr</i>	trochanter
<i>oc</i>	occiput	<i>v</i>	vertex



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PLATE X

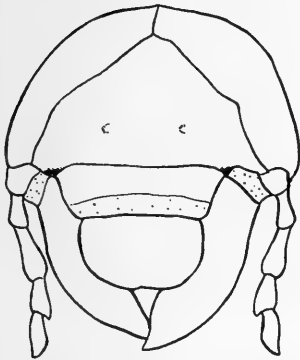
EXPLANATION OF PLATE X

CEPHALIC ASPECT OF HEAD; HYPOPHARYNX, STRIDULATING LEGS

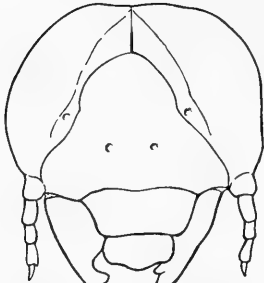
- Fig. 126. *Ochrosidia (Cyclocephala) immaculata*. Cephalic aspect of the head.
 Fig. 127. *Pinotus (Copriss) carolina*. Cephalic aspect of the head.
 Fig. 128. *Cotalpa lanigera*. Hypopharynx.
 Fig. 129. *Euphoria inda*. Hypopharynx.
 Fig. 130. *Canthon laevis*. Hypopharynx.
 Fig. 131. *Phyllophaga crassissima*. Hypopharynx.
 Fig. 132. *Ligyris gibbosus*. Hypopharynx.
 Fig. 133. *Anomala kansana*. Hypopharynx and mandibles showing their relation to each other.
 Fig. 134. *Anomala kansana*. Hypopharynx with pharynx attached.
 Fig. 135. *Ceruchus piceus*. Metathoracic leg showing stridulating surface on the trochanter.
 Fig. 136. *Ceruchus piceus*. Mesothoracic leg showing stridulating surface on the coxa.
 Fig. 137. *Passalus cornutus*. Meso- and metathoracic legs showing the stridulating modification.

ABBREVIATIONS EMPLOYED

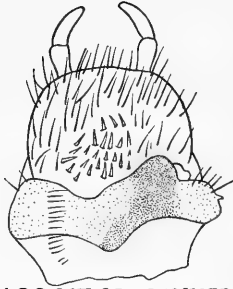
<i>cx</i>	coxa	<i>mtl</i>	metathoracic leg
<i>fm</i>	femur	<i>ph</i>	pharynx
<i>hc</i>	hypopharynx	<i>pta</i>	postcoila
<i>md</i>	mandible	<i>tt</i>	tibio-tarsus
<i>msc</i>	mesothoracic leg	<i>tr</i>	trochanter



126 OCHROSIDIA IMMACULATA



127 PINOTUS CAROLINA



128 COTALPA LANIGERA



129 EUPHORIA INDA



130 CANTHON
LAEVIS



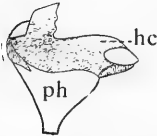
131 PHYLLOPHAGA
CRASSISSIMA



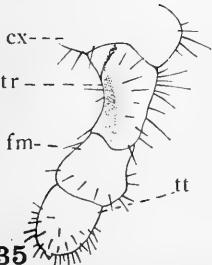
132 LIGYRUS GIBBOSUS



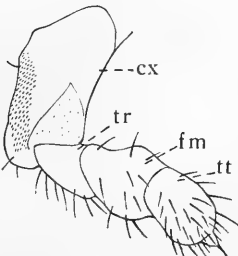
133 HYPOPHARYNX
AND MANDIBLES



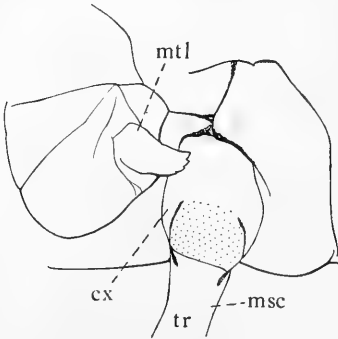
134 HYPOPHARYNX
AND PHARYNX



135 CERUCHUS PICEUS



136 CERUCHUS PICEUS



137 PASSALUS CORNUTUS

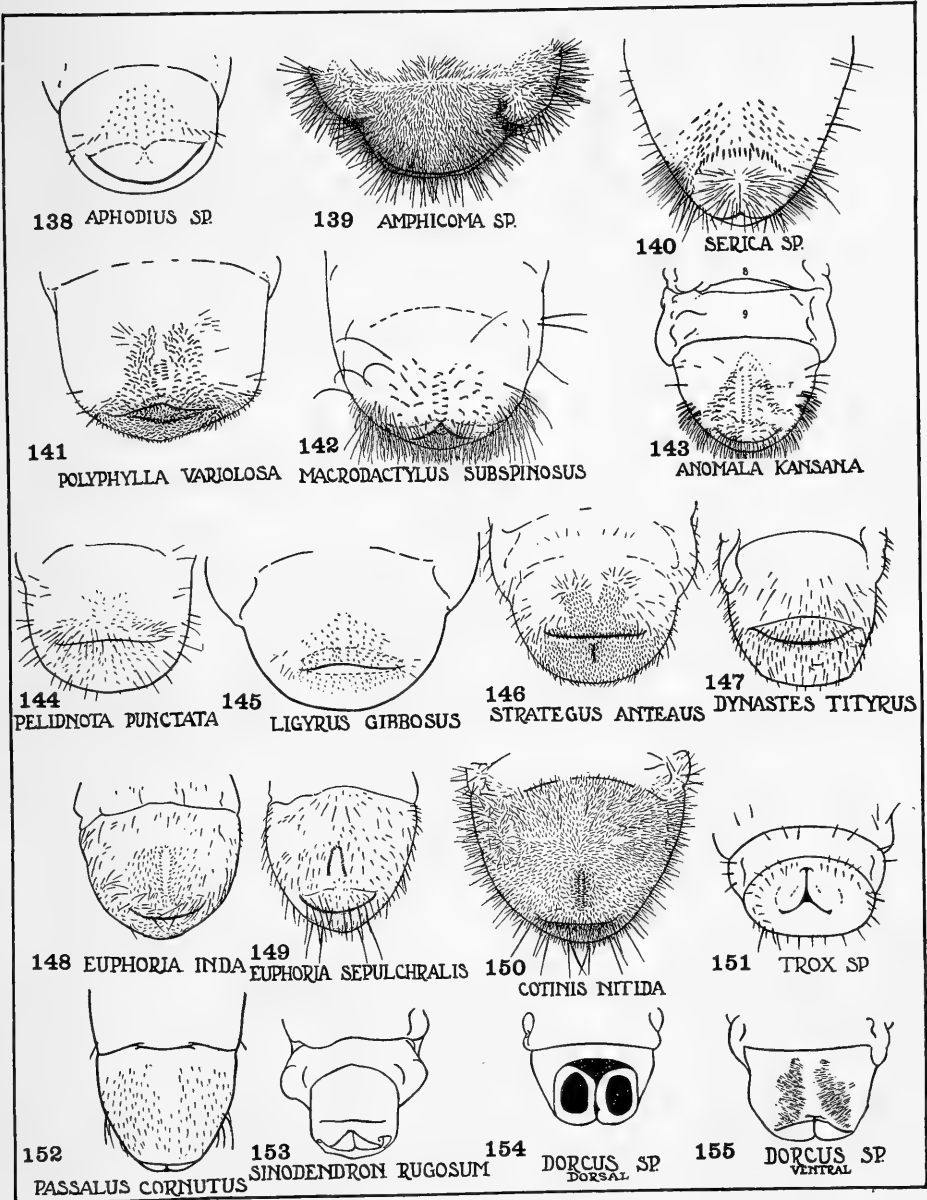
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PLATE XI

EXPLANATION OF PLATE XI

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT

- Fig. 138. *Aphodius* sp.
Fig. 139. *Amphicoma* sp.
Fig. 140. *Serica* sp.
Fig. 141. *Polyphylla variolosa*.
Fig. 142. *Macrodactylus subspinosus*.
Fig. 143. *Anomala kansana*.
Fig. 144. *Pelidnota punctata*.
Fig. 145. *Ligyris gibbosus*.
Fig. 146. *Strategus anteaues*.
Fig. 147. *Dynastes tityrus*.
Fig. 148. *Euphoria inda*.
Fig. 149. *Euphoria sepulchralis*.
Fig. 150. *Cotinis nitida*.
Fig. 151. *Trox* sp.
Fig. 152. *Passalus cornutus*.
Fig. 153. *Sinodendron rugosum*.
Fig. 154. *Dorcus* sp. (Dorsal).
Fig. 155. *Dorcus* sp. (Ventral).



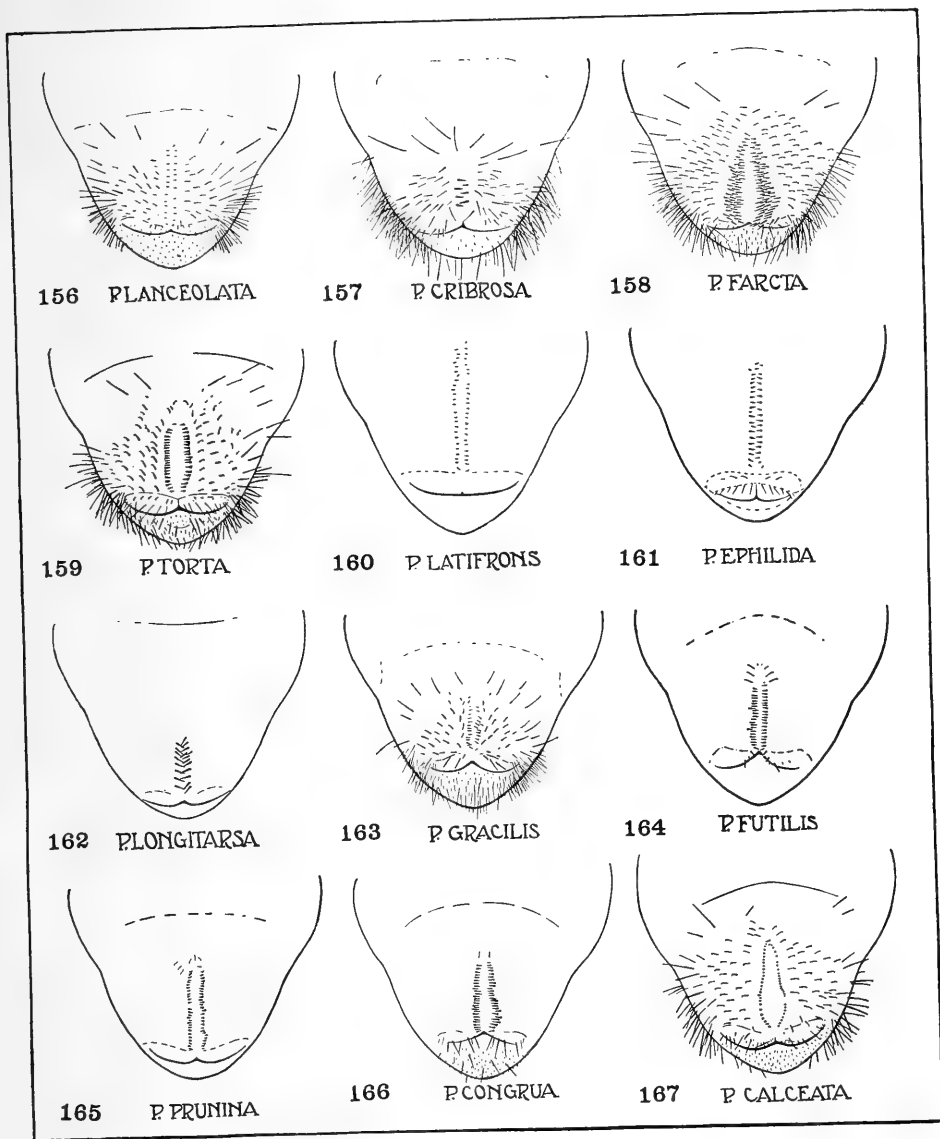
OF THE
UNIVERSITY OF CAMBRIDGE

PLATE XII

EXPLANATION OF PLATE XII

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA

- Fig. 156. *Phyllophaga lanceolata*.
Fig. 157. *Phyllophaga cribrosa*.
Fig. 158. *Phyllophaga farcta*.
Fig. 159. *Phyllophaga torta*.
Fig. 160. *Phyllophaga latifrons*.
Fig. 161. *Phyllophaga ephilida*.
Fig. 162. *Phyllophaga longitarsa*.
Fig. 163. *Phyllophaga gracilis*.
Fig. 164. *Phyllophaga futilis*.
Fig. 165. *Phyllophaga prunina*.
Fig. 166. *Phyllophaga congrua*.
Fig. 167. *Phyllophaga calceata*.



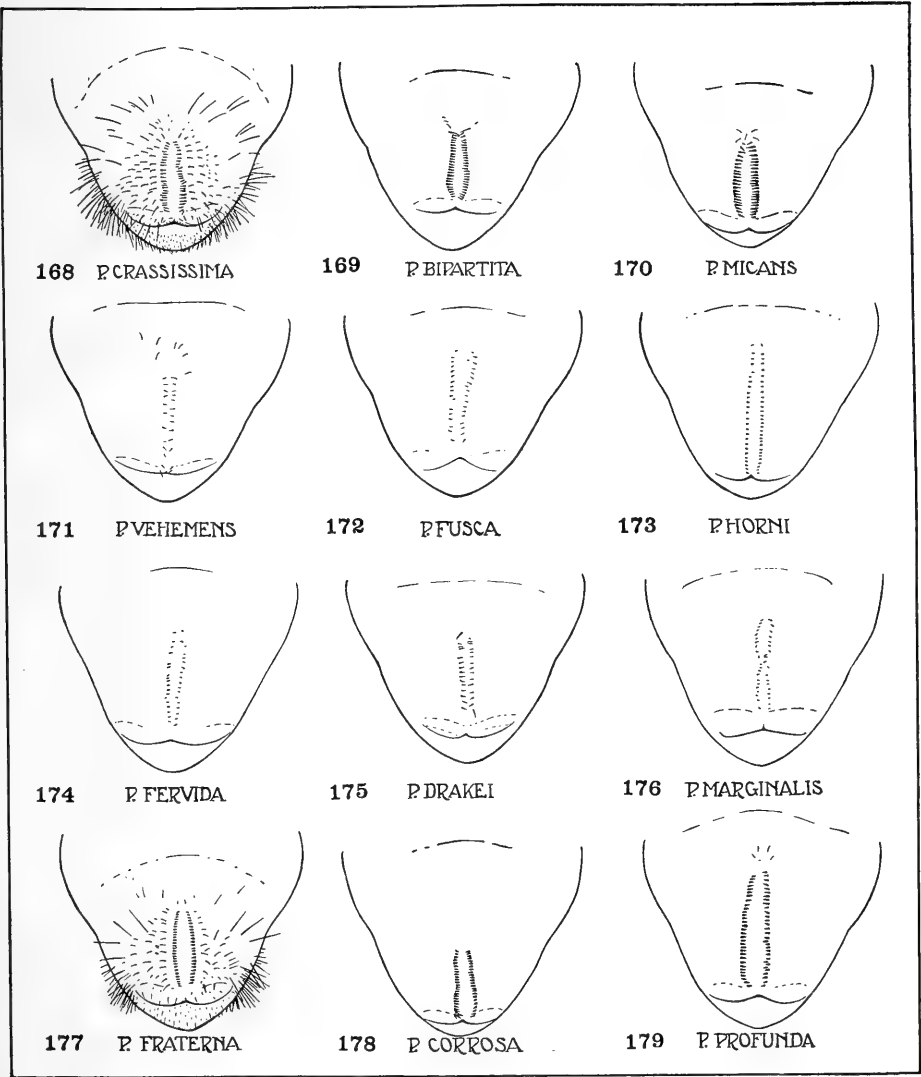
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PLATE XIII

EXPLANATION OF PLATE XIII

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA

- Fig. 168. *Phyllophaga crassissima*.
Fig. 169. *Phyllophaga bipartita*.
Fig. 170. *Phyllophaga micans*.
Fig. 171. *Phyllophaga vehemens*.
Fig. 172. *Phyllophaga fusca*.
Fig. 173. *Phyllophaga horni*.
Fig. 174. *Phyllophaga fervida*.
Fig. 175. *Phyllophaga drakei*.
Fig. 176. *Phyllophaga marginalis*.
Fig. 177. *Phyllophaga fraterna*.
Fig. 178. *Phyllophaga corrosa*.
Fig. 179. *Phyllophaga profunda*.



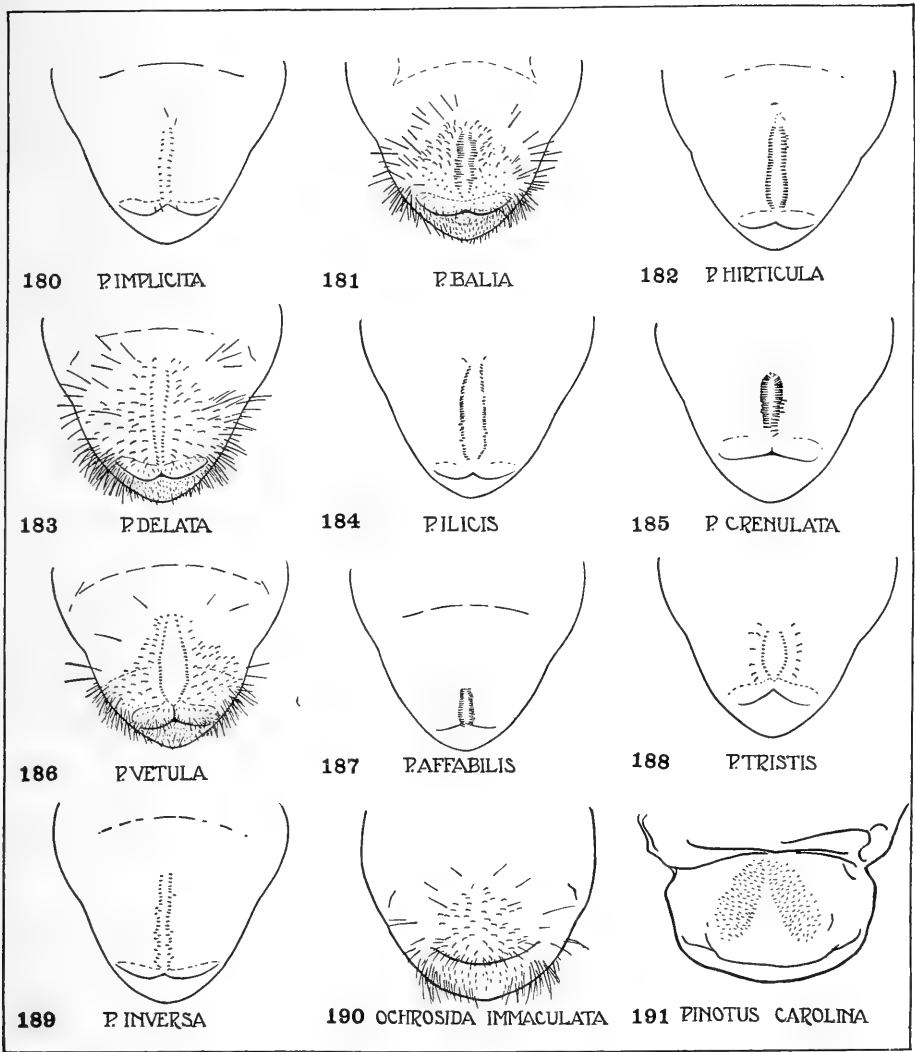
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PLATE XIV

EXPLANATION OF PLATE XIV

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA, OCHROSIDIA, AND PINOTUS

- Fig. 180. *Phyllophaga implicita*.
- Fig. 181. *Phyllophaga balia*.
- Fig. 182. *Phyllophaga hirticula*.
- Fig. 183. *Phyllophaga delata*.
- Fig. 184. *Phyllophaga ilicis*.
- Fig. 185. *Phyllophaga crenulata*.
- Fig. 186. *Phyllophaga vetula*.
- Fig. 187. *Phyllophaga affabilis*.
- Fig. 188. *Phyllophaga tristis*.
- Fig. 189. *Phyllophaga inversa*.
- Fig. 190. *Ochrosidia immaculata*.
- Fig. 191. *Pinotus carolina*.



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PLATE XV

EXPLANATION OF PLATE XV

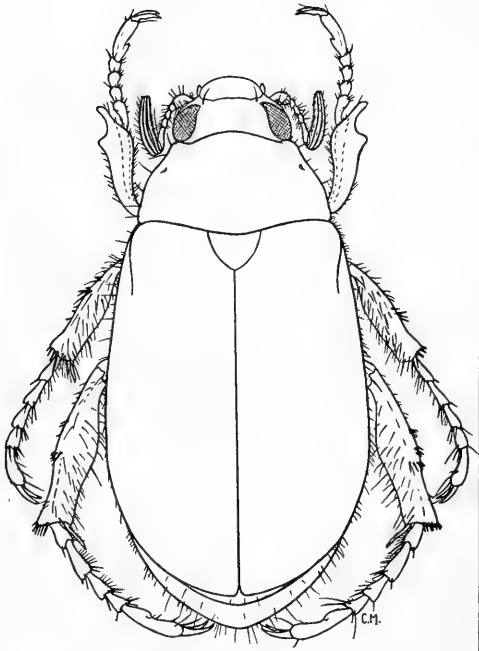
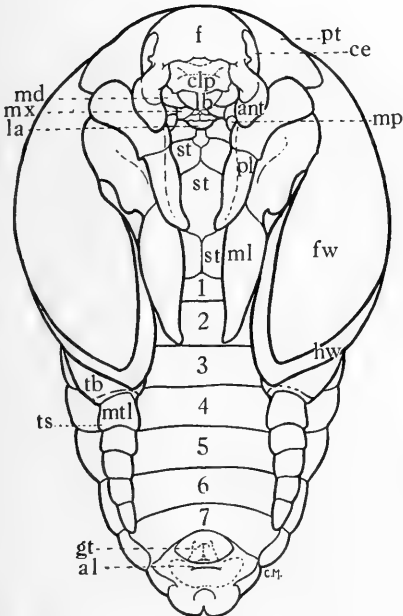
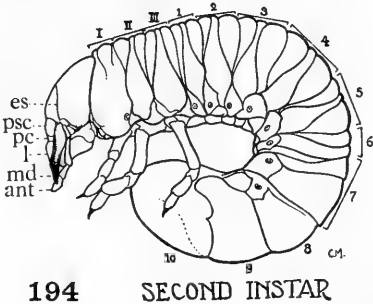
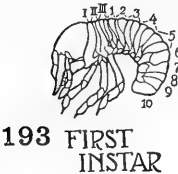
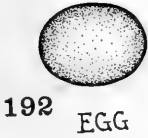
LIFE STAGES AND INSTARS OF A TYPICAL SCARABAEID, *Anomala kansana*
(For third instar of this species see figure 8, Plate II)

- Fig. 192. Egg stage.
Fig. 193. First larval instar.
Fig. 194. Second larval instar.
Fig. 195. Pupal stage.
Fig. 196. Adult stage.

ABBREVIATIONS EMPLOYED

<i>al</i> anal slit	<i>md</i> mandible
<i>ant</i> antenna	<i>ml</i> mesothoracic leg
<i>ce</i> compound eye	<i>mp</i> maxillar palpus
<i>clp</i> clypeus	<i>ml</i> metathoracic leg
<i>es</i> epicranial suture	<i>mx</i> maxilla
<i>f</i> front	<i>pc</i> preclypeus
<i>fw</i> fore wing	<i>pl</i> prothoracic leg
<i>gt</i> developing genitalia	<i>psc</i> postclypeus
<i>hw</i> hind wing	<i>pt</i> prothorax
<i>l</i> labrum of larva	<i>st</i> thoracic sterna
<i>la</i> labium	<i>ts</i> tarsal segments
<i>lb</i> labrum of pupa	<i>I-III</i> thorax
	<i>1-10</i> abdominal segments

ANOMALA KANSANA - LIFE STAGES



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